

C. W. BENSON

GAME AND FISHERIES DEPARTMENT,
CHILANGA, N.R.,

M. P. STUART IRWIN
NATIONAL MUSEUMS OF SOUTHERN
RHODESIA,

and C. M. N. WHITE
SECRETARIAT, LUSAKA.

The significance of valleys
as avian zoogeographical
barriers

SYNOPSIS

Consideration is devoted mainly to major valleys lying wholly or largely in the Federation of Rhodesia and Nyasaland, of which one or other of the authors has extensive personal experience. But an account is also included of the significance of the Albertine and Kenya Rifts. No attempt is made to discuss the more northerly Rifts, knowledge of which is probably insufficiently documented.

From a study of avian distribution, it is demonstrated that the Limpopo and Zambesi Valleys, and the Luangwa, Nyasa/Shire, Albertine and Kenya Rifts are all significant barriers to dispersal of species, due to the sharply different ecological conditions in the hot low-lying bottoms, compared to the higher ground on either side. Instances of subspecific differences are also given.

The position may be summarised as follows:—

			Number of species confined to—		number of subspecific differences on two sides*
			(a) South side	(b) North side	
Limpopo	..	..	15	31	15
Zambesi	..	..	8	35	30
			(a) West side	(b) East side	
Luangwa	..	..	22	8	9
Nyasa/Shire	..	..	19	4	13

Various anomalies are mentioned, such as subspecific differences on the two sides of the Nyasa/Shire Rift, with in some cases the western, in others the eastern, form the same as in Southern Rhodesia.

* In the case of the Luangwa and Nyasa/Shire, several instances of closely allied, geographically replacing, species-pairs included.

Discussion of the Albertine Rift is confined mainly to passerine species inhabiting evergreen forest. Thirty-two lowland species do not extend east of the Rift. The fauna of the montane areas of Kungwe, Marungu and Ufipa is relatively poor. The Kenya Rift is also an important barrier, being both an obstacle to the passage of certain species and an isolating factor which has resulted in the subspeciation of a number of species occurring on both sides.

INTRODUCTION

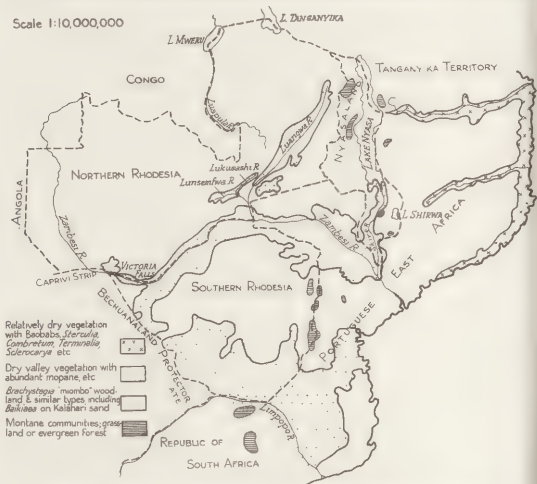
This paper focuses attention upon the faunistic significance of the Rift Valleys of Africa and some analogous gaps. Flint (1959), evidently referring to the Albertine and Kenya Rifts, writes that "Lower Pleistocene sediments locally postdate the main faulting: minor faulting has occurred even in very late Pleistocene times". Moreau (1952) has pointed out that the Pliocene was a period of much tectonic disturbance in Africa, but that only in the Pleistocene, and mainly in the last three quarters of a million years, did there develop the most marked rifting which gave rise to the levelling down in altitude of the floors of the present Lakes Nyasa, Tanganyika and Albert. The Kenya Rift took on its present form at the same period. In terms of geological time the Rift Valleys are thus recent formations, but as the review which follows indicates, their effect upon the distribution of birds is often pronounced, one inference being that the floors of these valleys are ecologically different from the country at higher levels on either side and, as such, provide an unfavourable biome to species living in the environments at higher levels. Thus the study of these valleys is of importance in the analysis of population systematics, since geographical isolates are often the apparent consequence of the rifts and similar valleys. It will be clear that there are enough geographical isolates in Africa of this type to allow for extensive speciation.

Apart from the fact that different subspecific isolates are to be found on either side of these valleys, it would appear that the valleys may have operated also as an absolute barrier to the dispersal of species. One obvious example of this appears to be provided by the Limpopo system, for a number of South Africa endemics have not crossed it to extend further north, whilst conversely tropical species extending south into Southern Rhodesia have not crossed it to extend still further south. Similar instances are given for the other examples discussed. The overall picture which emerges is that species characteristic of a particular biome are highly sensitive to ecological conditions provided by a different biome, and fail to cross it even though the actual gap is often only a few miles in width. This is of course wholly in keeping with the data set out by Moreau (1952) when he pointed out how birds tend to be strongly specific in Africa to certain main biotic types. Ornithologists have now demonstrated the truth of this in a number of ways: and evidence could be presented to show how speciation has occurred, or is apparently occurring, simply through populations of certain species having adopted different biomes, many instances of which are given by Benson *et al.* (1959). The field which still remains almost wholly untouched is to ascertain what factors associated with a given biome attach a particular bird species to it in a way which inhibits movement into or across another biome. In some of the most contrasting examples, as where montane forest species are separated by a dry area, one may suspect with good reason that certain very obvious problems of adjustment from high altitude, wet and shady montane forest to arid scrub will prove insurmountable obstacles, even though one cannot particularize about how such adjustments affect the organism. But in some of savanna instances this contrast must be considerably less severe, and it remains to explore just how the components of a biome do in fact interact with an organism to have such a profound inhibiting effect upon mobility.

Winterbottom (1959), in a general paper on the zoogeography of the South African avifauna, has discussed, necessarily only briefly, the significance of the Limpopo and Zambezi Valleys as barriers. His figures of species restricted by one or other of these valleys are all considerably higher than those given in the present paper. We have certainly been more

exacting in our inclusions. Thus Winterbottom gives 67 species as present in the Transvaal, but not in Southern Rhodesia. We give only 15 as having their northward range restricted by the Limpopo, but have included only those recorded as far north as the northern Transvaal (in eight cases positively recorded as only extending to the Zoutpansberg). Winterbottom was also at a disadvantage in that the work of Smithers *et al.* (1957) was not available to him when he wrote his paper. He concludes that neither the Limpopo nor Zambezi is an important faunal boundary. To be sure, 67 species out of a total of 497 for the Transvaal not occurring in Southern Rhodesia is only a small proportion. But nevertheless, disregarding such totals, it does seem that the numbers in the lists below are sufficiently high to suggest a considerable significance.

The Limpopo and the Zambezi are referred to as valleys, the remainder of the barriers



SIMPLIFIED VEGETATION MAP OF THE FEDERATION OF THE RHODESIAS & NYASALAND AND PORTUGUESE EAST AFRICA. ADAPTED FROM KEAY *ET AL.* (1959)

as rifts. According to Dr. G. Bond (*in litt.*), the middle Zambezi has been regarded by some authorities as a rift fault, but it can be shown beyond reasonable doubt that, irrespective of whether it is so or not, very little movement has taken place since the time of the early deposition of Kalahari sand. The surface on which the sand rests in the middle Zambezi has only been tilted about 300 feet in 300 miles since the sand was deposited, and it can be shown that the sand itself rests on an erosion bench, and banks up against a scarp which bounds this bench, not having been faulted by the movements which produced it. In the case of the middle Zambezi, therefore, movements are at least as old as mid-Tertiary. They were therefore much older than the movements already mentioned which occurred in areas further north. Also, according to King (1951: 207), no true rift valleys have been described south of the Sabi, and so, following this author, it is incorrect to refer to the Limpopo Valley as a rift.

The accompanying simplified vegetation map of the Federation largely follows Keay *et al.* (1959). But certain small areas shown by those authors as relatively dry or holding Mopane (types 20 and 22), in plateau country between Livingstone and Broken Hill, have been omitted. The predominant vegetation in this area is *Brachystegia* woodland, and Mopane is relatively scanty. The supposedly relatively dry areas shown between Lake Mweru and the south end of Lake Tanganyika, and west of the south end of Lake Nyasa, have also been omitted. In the former the annual rainfall-average is not less than 40 inches (*fide* map in Brelsford, 1960), with much Itigi thicket (type 12 in Keay *et al.*), while in the latter the average is not less than 32 inches, and the vegetation is mainly *Brachystegia*, at an altitude of not less than 4,000 feet, with some small scattered patches of evergreen forest at over 6,000 feet (Benson, *in litt.*). The dry areas in the littoral of Portuguese territory north of the Zambezi are differentiated from Mopane areas, as indeed they are by Keay *et al.* But it is worth mentioning that Pedro & Barbosa (1955) do not mention *Colophospermum mopane* from this area at all, while Vincent (1934: 149) describes the country behind the mouth of the Lurio River as consisting of park-like thorn scrub.

It will be noticed that, more especially in the Luangwa and Nyasa/Shire lists, various generic names have been added in brackets. This arises from recent changes in nomenclature, in accordance with a broader concept of the genus, rendering in this respect Benson (1953) particularly out of date. The insertion of such names, which have become in effect subgenera, will assist in tracing information referred to.

THE LIMPOPO VALLEY

The low-lying drainage of the Limpopo Valley constitutes a most effective barrier to dispersal. North of the Limpopo River the Southern Rhodesia plateau runs in a north-easterly direction, sloping gradually towards the south-east so that large areas of the country lie below 3,000 feet, and to well below 1,000 feet in the extreme east. Two factors play a part in this region; arid Mopane country predominates from about 28° E., but elsewhere to the west on to the plateau areas of the Bechuanaland Protectorate there is a gradual transition to a wooded steppe with abundant *Acacia* and *Commiphora*; this, accompanied by a faunal change, prevents any southward extension of the plateau avifauna that is elsewhere isolated only by the presence of the ecologically unsuitable valley areas.

The region as a whole contains the most arid country to be found in any of the areas under discussion, the annual rainfall-average being in general less than 16 inches (see map in Brelsford, 1960).

On the South African side of the valley similar conditions prevail until the Transvaal highveld is reached, when one encounters the Zoutpansberg Mountains, reaching an altitude of over 5,000 feet, where true montane forest again makes its appearance, and there are considerable areas of montane grassland (see Keay *et al.*, 1959). This region generally marks the northernmost limit of the typically endemic South African avifauna,

of which only a few constituent species reach the highlands of eastern Southern Rhodesia. There is also a continuation of the low-veld vegetation in the extreme north-eastern Transvaal and the Kruger National Park. Further south, the considerable area of evergreen forest existing at Woodbush marks the southernmost limit of *Malacometus nigrifrons*, apparently as yet unrecorded from the Zoutpansberg further to the north.

Mention may also be made here of the dry Sabi Rift, where again the annual rainfall-average drops to below 16 inches. But the only evidence of it being a barrier to avian dispersal is in the case of *Psaltidoprocne holomelaena*, with which *P. orientalis* has been made conspecific by White (1961). Following Irwin (in press for *Bull. Brit. Orn. Cl.*, 81, 1961), *P. h. holomelaena* occurs on the high ground of the Bikita and Zimbabwe areas west of the Rift, where there is high rainfall, with rich *Brachystegia* woodland and relic evergreen forest. *P. h. orientalis* occurs on the opposite side of the Rift, and in eastern Southern Rhodesia generally, ranging regularly west to Rusape and Inyazura. It has also been recorded south of the Birchenough Bridge on the Sabi River, probably as a wanderer.

The information which follows in regard to the Limpopo Valley acting as a barrier is derived mainly from McLachlan & Liversidge (1957) for the southern side, and Smithers *et al.* (1957, as amended 1959) for the northern side. Attention may be drawn in particular to 15 species frequenting *Brachystegia* woodland on the northern side, but absent on the southern side, where this habitat does not exist. On the other hand several species are mentioned as occurring in this habitat in Southern Rhodesia, but in other types of woodland south of the Limpopo.

A. SPECIES WHOSE RANGE IS RESTRICTED BY THE LIMPOPO VALLEY

(1) *Occurring only on the southern side*

Several of the species in this section occur north of the Zambezi, but are included as they are unknown in Southern Rhodesia.

1. *Geocolaptes olivaceus*: Represents a genus endemic to the Republic of South Africa, frequenting open country, ranging to the northern Transvaal.

2. *Mesopieops griseocephalus*: *M. g. griseocephalus*, associated with evergreen forest, extends as far north as Woodbush (Selater, 1911). No record has been traced from the Zoutpansberg, where it might also be expected. It does not occur in southern Nyasaland. As indicated by McLachlan and Liversidge (1957). The species is unknown in Southern Rhodesia, possibly due to competition with *Campethera abingoni* (see Smithers *et al.*, 1959). Another subspecies, however, occurs in the north of Northern Rhodesia and Nyasaland (Benson and White, 1961).

3. *Anthus leucophrys*: Although reappearing north of the Zambezi (Zambezi list A (2)), unknown in Southern Rhodesia, but extending from the Cape Province to the northern Transvaal, in open grasslands. Although it occurs in the Sul do Save (Pinto and Lamm, 1953-56), no evidence has been traced of its extensive occurrence in Portuguese East Africa as indicated by McLachlan and Liversidge (1957).

4. *Lioptilus nigricapillus*: Extends north to the Zoutpansberg, inhabiting evergreen forest edges. The genus is also represented in the eastern Congo and Ruanda-Urundi (Chapin, 1953).

5. *Monticola rupestris*; 6. *M. explorator*: Both reach their northern limit in the northern Transvaal, and inhabit open, rocky country.

7. *Oenanthe monticola*: 8. *Myrmecocichla bifasciata*: Both reach their northern limit in the Zoutpansberg and inhabit arid hilly country.

9. *Cossypha dichroa*: Extends north to the Zoutpansberg, in evergreen forest.

10. *Cisticola textrix*: Ranges in open grasslands north to the northern Transvaal;

reappears in the north-west of Northern Rhodesia and in Angola (Benson and White, 1961).

11. *Prinia maculosa*: Finds its northern limit in the Zoutpansberg, inhabiting short bushes in open country.

12. *Spreo bicolor*: Extends in open country to the northern Transvaal.

13. *Nectarinia afra*: Ranges to the northern Transvaal, usually on forest edges. Supposedly conspecific forms occur in eastern Africa, south to the Nyika plateau in northern Nyasaland, and in western Angola, but further investigation is needed as to their true relationship to *N. afra*.

14. *Ploceus capensis*: Extends north to the Zoutpansberg, in almost any type of country where there are trees or bushes, usually near water. Unknown anywhere directly to the north, possibly due to competition with *P. xanthops* (see Benson and White, 1961). It is however represented in Angola and extreme north-western Northern Rhodesia by *P. c. temporalis*.

15. *Serinus scotops*: Extends north to the Zoutpansberg, mostly on the edges of evergreen forest. Specimens of this species and *S. citrinelloides* (see Zambezi list A (2)) have been compared. In plumage they are very similar. The most marked difference is the stouter bill of *S. scotops*, with curved, rather than straight, culmen and keel to lower mandible. In habitat they are apparently analogous. Their relationship is sufficiently close to regard them as at least representing a single superspecies.

(2) *Occurring only on the northern side*

It is convenient to treat the much larger number of species in this section (31) than in (1) above (15) in rough ecological categories.

Brachystegia woodland

1. *Buccandon whytii*: Frequents well developed woodland on the Mashonaland plateau above 3,500 feet, south to Melsetter.

2. *Prodotiscus insignis*: Known from scattered localities above 3,000 feet, from west of the Victoria Falls, as far south as Selukwe in the Midlands, and in the east of Southern Rhodesia.

3. *Campethera cailliautii*: Occurs up to 3,500 feet in rich woodland in the east of Southern Rhodesia, south to Mt. Selinda. There is also a distinct, apparently relic, population at Funhalouro in the Sul do Save (Pinto, 1960).

4. *Hyhota australis*: Widespread above 3,000 feet in Southern Rhodesia to as far south as the Matopos, but unknown west of about 28° 30'. Also collected in *Acacia xanthophloea* trees at 500 feet at the Sabi Lundi confluence, and recorded from Coguno in the Sul do Save (Lamm, 1953).

5. *Monticola angolensis*: Throughout Southern Rhodesia above 3,500 feet, occasionally to 2,000 feet.

6. *Sylvietta whytii*: Occurs in eastern Southern Rhodesia as far south as Mt. Selinda, again along the northern fringe of the Mashonaland plateau and south-west to Matabeleland, where it inhabits Baikiaea woodland.

7. *Cisticola brachyptera*: Mostly in secondary growth below 4,000 feet, on the eastern border, south to Chipinga.

8. *Heliolais erythroptera*: Much as for the last species, south to Mt. Selinda.

9. *Parus griseiventris*: Inhabits well developed woodland above 3,500 feet, on the eastern border, south to Mt. Selinda. Unknown further west than about 30° 25'. Although known from Baikiaea woodland at Livingstone (Benson, 1960), it is still unknown from the Southern Rhodesian side in such an association. Regarded as a species distinct from *P. afer* (Hall & Traylor, 1959; Irwin, 1959).

10. *Parus rufiventris*: Distribution in Southern Rhodesia as for the last species, though occurs as low as 2,000 feet.

11. *Lamprotornis chloropterus*: General, except that apparently only a seasonal wanderer to southern Matabeleland. Recorded as far south as the mouth of the Save (Pinto & Lamm, 1956).

12. *Anthreptes longuemarei*: Throughout the eastern border, where it occurs down to 2,000 feet in rich woodland. Elsewhere on the plateau only usually above 3,500 feet, and unknown west of 30° 25'.

13. *Salpornis spilonta*: Restricted to rich woodland on the plateau as far south as the Selukwe District and Bikita above 3,000 feet, but unknown west of the Sengwa River, and not so far recorded on the eastern border.

14. *Serinus mennelli*: Occurs on the plateau above 3,000 feet in Baikiaea as well as Brachystegia woodland, just reaching Bechuanaland at Panda Matenga (Hall, 1956). In eastern Southern Rhodesia, found as low as 2,000 feet.

15. *Emberiza cabanisi*: Ranges in rich woodland as far south as the Midlands, and in the east to Melsetter, usually above 3,000 feet, though lower in the east.

It is worth mentioning that the following species, characteristic of Brachystegia woodland in Southern Rhodesia, nevertheless occur in other types of woodland south of the Limpopo:—*Anthus similis*, *A. lineiventris*, *Coracina pectoralis*, *Eremomela scotops*, *Cisticola aberrans*, *Nectarinia chalybea* and *Serinus gularis*. However, *Anthus lineiventris* and *Cisticola aberrans* are essentially associated with a rocky habitat both to the north and south of the Limpopo. *Coracina pectoralis* and *Eremomela scotops* have in fact both also been found associated with *Acacia xanthophloea* trees at the Sabi/Lundi confluence, and recently Irwin has found *Eremomela scotops* common alongside *E. usticollis* in alluvial Acacia growth on the lower Nuanetsi River at 22° 02'S., 31° 25' E., seemingly replacing *E. icteropygialis*.

Evergreen forest

All seven of the following species are confined in Southern Rhodesia to the eastern border.

16. *Bycanistes brevis*: South to Mt. Selinda, between 2,000 and 7,000 feet.

17. *Andropadus milanensis*: General between 2,000 and 7,000 feet.

18. *Trochocercus albonotatus*: Represented in this area by an endemic subspecies, ranging from 3,500 to 7,000 feet.

19. *Pogonochila swynnertoni*: A distinctive endemic species, ranging from 3,000 to 5,000 feet.

20. *Apalis (melanocephala) chirindensis*: Usually regarded as conspecific with *A. melanocephala*, but perhaps best treated as an endemic species, probably overlapping with the distinctly coloured *A. m. lightoni* at the southern end of the Chimanimani Mts. *A. (m.) chirindensis* occurs between 2,000 and 7,000 feet.

21. *Prinia robertsi*: A distinctive endemic species, common between 4,000 and 7,000 feet, mostly on forest edges and in secondary growth.

22. *Cryptospiza reichenovii*: Between 4,000 and 7,500 feet. Certain lowland species, none of which occur higher than 2,000 feet in eastern Southern Rhodesia, are not formally included. These are *Phyllastrephus debilis* and *Bias musicus*, extending south in Portuguese East Africa to Inhambane; and *Prionops scopifrons* and *Pirenestes minor*, south to Beira. For particulars of the distribution of *Apalis melanocephala lightoni*, see Zambezi list B.

Miscellaneous

23. *Apus myoptilus*: Known from cliff-faces at Inyanga and on the Chimanimani Mts.

23a. *Apus aequatorialis*: Frequents cliff-faces as far south as Mashonaland and eastern Southern Rhodesia, wandering as far south as Bulawayo.

THE SIGNIFICANCE OF VALLEYS AS AVIAN ZOOGEOGRAPHICAL BARRIERS

24. *Pinarornis plumosus*: Ranges from Fort Jameson and Petauke, in Northern Rhodesia, south-west to Bulawayo, in association with rocky kopjes. The record from the Percy Fyfe Nature Reserve, south of the Limpopo (van der Merwe and Pienaar, 1959), cannot be accepted.

25. *Cisticola cantans*: Inhabits bracken growth, south to Mt. Selinda, west to Rusape. Specimens from Selukwe, on the basis of which it was recorded by Smithers *et al.* (1957), are actually attributable to *C. aberrans*, nor has its occurrence at Salisbury been substantiated (C. J. Vernon, *in litt.*).

26. *Sphenocercus (Melocichla) mentalis*: In Southern Rhodesia, confined to the eastern border below 3,500 feet, south to Mt. Selinda, inhabiting rank grass growth near streams. Generic name in accordance with White (1960d).

27. *Tchagra minuta*: Range and habitat similar to that for the last species.

28. *Nectarinia kilimensis*: In Southern Rhodesia, confined to the eastern border above 4,500 feet, mainly in bracken growth on the edge of evergreen forest.

29. *Nectarinia venusta*: Disregarding a population in the Zambezi Valley, confined in Southern Rhodesia to the eastern border; unknown west of Macheke, ranging from 1,000 to 7,500 feet, habitat as for the last species.

30. *Euplectes hordeaceus*: Ranges south to Mt. Selinda, extending west to Inyazura. Inhabits rank grass with herbaceous growth below 4,000 feet.

31. *Euplectes macrourus*: Inhabits wet short grasslands on the Mashonaland plateau to as far south as Selukwe and Chatsworth.

32. *Oryzopsis locustella*: Habitat and distribution similar to that for the last species.

B. SUBSPECIFIC DIFFERENCES ON THE TWO SIDES OF THE VALLEY

1. *Tauraco persa* (= *T. corythaix*): A population akin to *T. p. corythaix*, but not identical, occurs as far north as the Zoutpansberg. In eastern Southern Rhodesia it is replaced by *T. p. livingstonii*. Habitat evergreen forest and dense thickets. For further details, see Moreau (1958).

2. *Batis capensis*: An evergreen forest species; *B. c. capensis* north to the Zoutpansberg, *B. c. erythrophthalma* in eastern Southern Rhodesia.

3. *Turdus olivaceus*: Habitat as for the last; *T. o. transvaalensis* in the northern Transvaal, *T. o. swynnertoni* in eastern Southern Rhodesia.

4. *Phylloscopus ruficapilla*: Habitat as for the last; *P. r. johnstoni* in eastern Southern Rhodesia, *P. r. ruficapilla* in the Zoutpansberg.

5. *Bradypterus barratti*: Habitat as for the last; *B. b. barratti* in the northern Transvaal, *B. b. priestii* in eastern Southern Rhodesia.

6. *Apalis thoracica*: Associated with evergreen forest and thickets; *A. t. spelonkensis* in the Zoutpansberg, *A. t. arnoldi* in eastern Southern Rhodesia, *A. t. rhodesiae* further west.

7. *Cisticola aberrans*: Apparently always associated with rocks (see also above); *C. a. aberrans* in the Transvaal, *C. a. nyika* in Southern Rhodesia.

8. *Hirundo fulgula*: Associated with rock-faces; *H. f. fulgula* in the Transvaal, *H. f. fusciventris* in Southern Rhodesia (and northwards across the Zambezi Valley, which forms no such marked barrier as the Limpopo; note that *H. f. rufigula* in Benson, 1953 is the same as *H. f. fusciventris*, following White, 1957).

9. *Malaconotus olivaceus*: An evergreen forest species; *M. o. olivaceus* in the northern Transvaal, *M. o. makawa* in eastern Southern Rhodesia.

10. *Nectarinia chalybeata*: *N. c. subalaris* in the Transvaal, with apparently no marked habitat preference; *N. c. manoensis* in Southern Rhodesia, more especially in Brachystegia woodland.

11. *Promeropops gurneyi*: Associated with Protea bushes; *P. g. gurneyi* in the northern Transvaal, *P. g. ardens* in eastern Southern Rhodesia.

12. *Lagonosticta rubricata*: Commonly in bracken growth on the edge of the evergreen forest; *L. r. rubricata* in the northern Transvaal, *L. r. haematocephala* in eastern Southern Rhodesia.

13. *Serinus sulphuratus*: Habitat not clearly definable, but often near water; *S. s. wilsoni* in the Transvaal, *S. s. sharpii* in eastern Southern Rhodesia.

14. *Fringillaria capensis*: A rock-dweller; *F. c. limpopoensis* in the Zoutpansberg, *F. c. plowesi* in Southern Rhodesia, replaced by *F. c. smithersii* in the Chimanimanu Mts. For a discussion of the phylogeny of the various more northern subspecies, see Irwin (1958).

15. *Estrilda melanotis*: edge of evergreen forest and rank growth. *E. m. melanotis* ranges as far north as the Zoutpansberg, in eastern Southern Rhodesia it is replaced by the very different *E. m. kilimensis*. A black-faced form similar to that found in South Africa has once been recorded from the Matopos, but its status as a wild population seems to be in some doubt.

16. *Sarothrura a. affinis* has been recorded from the eastern Cape Province, *S. a. antonii* from eastern Southern Rhodesia. It is not included above because there are apparently still no records of either from the Transvaal.

To this list must be added *Buteo rufofuscus*: Inhabits mountainous or hilly country; *B. r. rufofuscus* ranges as far north as the Zoutpansberg and also to northern South West Africa. *B. r. augur* on the other hand replaces it northwards from the plateau of Southern Rhodesia to Abyssinia.

THE ZAMBEZI VALLEY

The sector for consideration is that between the Victoria Falls and the Indian Ocean. It is convenient to divide it into two sub-sectors and to treat them separately:

- (a) Above Chemba, on the river at about 35° E.; generally a well marked escarpment on either side of the valley; conditions relatively arid, Mopane woodland predominating.
- (b) Below Chemba, escarpment not so well marked, while towards the entrance of the river to the sea there are hundreds of miles of country below 600 feet, both to the north and south; conditions more humid, *Brachystegia* replacing Mopane.

Considering sub-sector (a), for some 60 miles below the Falls the Zambezi flows through narrow rocky gorges, below which a valley floor fans out, as much as 30 miles across in places. The general altitude of the floor in the upper reaches is about 1,300 feet, gradually descending to less than 600 feet near Tete. For the most part there is a well marked escarpment on either side of the valley, the top of which is 2,000–3,000 feet above the floor. Various rivers cut through the escarpment, such as the Gwaai and the Sanyati on the southern side, while much the most important on the northern side is the Luangwa.

The annual rainfall-average between the Victoria Falls and Kariba is 16–24 inches, between Kariba and Chicowa 24–32, dropping again around Tete to 16–24, rising again towards Chemba to 24–32. The figures for plateau country on either side above the valley average higher. North of the area between the Victoria Falls and Chirundu a 32–40 inch isohyet is attained, and near Furancungo (north of Tete) even 48–56.

The characteristic vegetation of the valley is Mopane woodland, intersected by alluvial *Acacia* growth. But there are also extensive areas of dense thicket, particularly well developed between Kariba and Chirundu. The vegetation is in general contrast to that on the plateau country on either side, where *Brachystegia* woodland predominates. However, there is Mopane on the plateau in the arid west of Southern Rhodesia, and likewise in relatively small scattered pockets in the Southern Province of Northern Rhodesia. Here, such birds as *Tockus erythrorhynchus*, *Lamprotornis mevesii* and *Plocepasser mahali*, so characteristic of the valley, are liable to occur.

At Kariba, relatively high ground, rising to over 2,500 feet, closes in on the river gorge. The vegetation is *Brachystegia* woodland, as in plateau country. Although these hills have not been worked ornithologically, their avifauna is probably rather depauperate, with many typical plateau *Brachystegia* species absent.

Considering sub-sector (b), the contrast to (a) is marked. Towards the coast there is a broad belt of country where the annual rainfall-average does not drop below 40 inches, while north and south of the Zambezi mouth it rises to 48 inches, and at Beira the isohyet is even 56-64 inches. This increase in humidity is reflected in the vegetation. According to Pedro & Barbosa (1955), Mopane woodland does not extend appreciably further east than Chemba, and there is a practically continuous belt of *Brachystegia*, from eastern Southern Rhodesia through the coastal littoral to Mlanje, in southern Nyasaland. Between Beira and the Zambezi mouth, too, there are even pockets of evergreen forest, judging from some of the trees listed by these authors.

The foregoing is derived from:—Anon. (1960); Brelsford (1960) (rainfall-map); Pedro & Barbosa (1955); Trapnell *et al* (1948); and Trapnell & Clothier (1957). The lists of birds below to which the Zambezi Valley acts as a barrier have been obtained mainly from Benson (1953); Benson & White (1957); Smithers *et al.* (1957, as amended 1959); and Vincent (1933-36). Any specimens particularly mentioned are in the National Museum, Bulawayo.

Before proceeding to these lists, however, some discussion is necessary as to the possibility of a connection above the Victoria Falls or through the humid sea-littoral. At the end of list B below (subspecific differences) there is a further list of species showing no differentiation on the two sides of the valley even though there is no evidence of any gene-flow. On the other hand, some species which are generally absent below the Falls do link up above, through an area of poorly developed *Brachystegia* as well as *Baikiaea* woodland. In Southern Rhodesia and the Southern Province of Northern Rhodesia, the more specialised *Brachystegia* species do not range as far west as the Falls, on either side of the Zambezi. But examples of those which do are *Anthus similis*, *Coracina pectoralis*, *Bradornis pallidus*, *Eremomela icteropygialis*, *E. scotops*, *Camaroptera stierlingi*, *Cisticola fulvicapilla* (recent study shows the populations of Southern Rhodesia and the south of Northern Rhodesia to be very similar, with *C. f. hallae* extending from the Falls westwards), *Anthoscopus caroli* (with the qualification that recently a specimen apparently representing a distinct subspecies has been collected at Feira), and *Serinus mennelli*. Examples from other habitats are *Lanius melanoleucus* (excepting a record by Benson & White, 1957: 161) and *Ortygospiza atricollis*.

With regard to the possibility of a connection through the humid sea-littoral between eastern Southern Rhodesia and Mlanje, in southern Nyasaland east of the Nyasa Shire Rift, in list B below there is the case of *Apalis melanocephala lightoni* among evergreen forest forms, while the populations of *Andropadus m. milanensis* could have been linked up in a colder climate (there is no evidence of any link at the present time). Among *Brachystegia* forms, under colder conditions there could have been a link between the populations, apparently now separated, of *Parus rufiventris pallidiventris* and *Anthreptes longuemareyi nyassae*. On the other hand, this does not explain, for example, the case of *Buccanodon whytii sowerbyi* or *Apalis thoracica arnoldi*, for which it seems necessary to postulate a link further up the valley, where Mopane now predominates. To take another type of example, *Parus griseiventris*, in which no subspecies are recognized, at the present time is confined in Southern Rhodesia to the eastern part, but occurs in Northern Rhodesia as far south as Livingstone (Limpopo list A(2)). In Nyasaland it is only known on the west of the Nyasa Shire Rift. In this case it seems necessary to postulate a connection between eastern Southern Rhodesia and Livingstone under more humid conditions.

A. SPECIES WHOSE RANGE IS RESTRICTED BY THE ZAMBEZI VALLEY

(1) *Occurring only on the southern side*

1. *Columba guinea*: Widespread on rocky hills in Southern Rhodesia. Although it reappears in eastern Africa, to as far south as the Rukwa Valley (Vesey-Fitzgerald & Beesley, 1960), it is unknown in Northern Rhodesia, Nyasaland or Portuguese East Africa north of the Zambezi.

2. *Macronyx capensis*: Inhabits wet grasslands above 3,000 feet in Southern Rhodesia, but unknown further north. Incidentally, it occurs throughout the Inyanga area above 4,000 feet, but is replaced below this level by *M. croceus*. At Chimanimani only the latter is found, occurring up to 6,000 feet, and as low as 500 feet at the Sabi-Lundi confluence.

3. *Bessonoris humeralis*: The northernmost limit of the range is the top of the southern escarpment of the Zambezi Valley. A thicker dweller, widespread in Southern Rhodesia.

4. *Sphenoeacus afer*: Unknown north of Inyanga. Confined in Southern Rhodesia to the east of the territory, typically inhabiting rank bracken growth.

5. *Eurocephalus anguitimens*: Typically, inhabits thorn country and Brachystegia edges on the plateau of Southern Rhodesia (*E. a. anguitimens*), but unknown north of the Zambezi south of the Rukwa Valley (Vesey-Fitzgerald & Beesley, 1960), where the form is presumably *E. a. ruppelli*.

6. *Promerops gurneyi*: Unknown north of eastern Southern Rhodesia, where associated with Protea bushes. *P. g. ardens* is endemic to this area.

Mention has already been made of *Pogonocichla swynnertoni* and *Prinia robertsi*, endemic to the evergreen forests of eastern Southern Rhodesia. *Apalis (melanocephala) chirindensis* (see also under list of subspecific differences), is another endemic, so distinct and occurring so close to *A. m. lightoni*, that it is perhaps also best regarded as a species. They will probably prove to overlap at the south end of the Chimanimani Mts. between 1,000 and 2,000 feet.

(2) *Occurring only on the northern side*

It is convenient to treat the much larger number of species in this section (35) than in (1) above (8) in rough ecological categories.

Brachystegia woodland

The following list could be increased considerably by the inclusion of various further species widespread in the north of Northern Rhodesia and in some cases in Nyasaland as well. But as none of them occur south of 14°, and so do not approach at all closely the low lying ground of the Zambezi their inclusion is not appropriate. It is particularly noteworthy that there is not a single Brachystegia species occurring in Southern Rhodesia which is not represented to the north of the Zambezi.

1. *Tockus pallidirostris*: In Southern Nyasaland to the Port Herald District (Long, 1960-61); in Northern Rhodesia to as far south as Rufunsa, the Kafue River at 15° 50' S., 28° 20' E. (recent specimen), though unknown in the Southern Province.

2. *Ipophilus stierlingi*: Occurs near the southern extremity of the Nyasa/Shire Rift on both sides, in Nyasaland, and in Portuguese East Africa (Vincent, 1933-36).

3. *Muscicapa (Myopornis) boehmi*: See Nyasa Shire list A (1), though west of the Luangwa Rift unknown south of Broken Hill.

4. *Hylia flavigaster*: An excellent example, occurring extensively on both sides of the Nyasa/Shire Rift, and in Northern Rhodesia collected as far south as the Kalomo District (Benson, 1958), and recently on the lip of the escarpment in the Choma District at 17° 00' S., 27° 20' E.

5. *Elminia albicauda* (= *Erannornis longicauda*): See Nyasa/Shire list A (1), though west of the Luangwa Rift unknown south of about 14°.

6. *Erythropygia barbata*: See Nyasa/Shire List A (1), but west of the Luangwa Rift unknown south of 14° 40' (Benson *et al.*, 1959).

7. *Sylvietta ruficapilla*: See Nyasa/Shire List A (1), while west of the Luangwa Rift collected in the Kalomo District (Benson, 1958) and recently on the lip of the escarpment in the Choma District, at 17° 00' S., 27° 20' E. An excellent example.

8. *Lanius souzai*: Present near the southern extremity of the Nyasa Shire Rift on both sides. West of the Luangwa Rift, extends as far south as Lusaka and the Sesheke District, but unknown in the Southern Province (Benson, 1959). The statement by Vincent (1952) that it occurs in the "mid-Zambezi valley" appears to be based on his record (1935) from Furancungo in plateau country well north of the valley.

9. *Nectarinia shelleyi*: The type-locality of *N. s. shelleyi* is from the Zambezi Valley, whence there is no subsequent record. The two specimens collected by Alexander may have been wanderers from plateau country to the northward. The species occurs uncommonly on both sides of the Nyasa/Shire Rift, and in Northern Rhodesia south to Kalomo and Livingstone.

10. *Antheptes anchietae*: See Nyasa Shire List A (1); though west of the Luangwa Rift unknown south of Broken Hill.

11. *Ploceus (Phormoplectes) olivaceiceps*: Present on both sides of the Nyasa/Shire Rift, but unknown south of the Zambezi, except that Clancey (*in litt.*) has recently obtained it at Panda in the Sul do Save.

Mention should also be made of *Lybius leucomelas frontatus*, which it is in fact perhaps arguable is a distinct species. This particular form inhabits Brachystegia, whereas all other forms prefer by contrast thornveld. *L. l. frontatus* and *L. l. centralis* show evidence of secondary hybridization rather than clinal intergradation near Livingstone (Benson & White, 1961). Typical *L. l. frontatus* is widespread in Northern Rhodesia west of the Luangwa Rift and three specimens of it have recently been collected near Choma at 16° 39' S., 27° 01' E. For the position further east see Nyasa/Shire List A (1).

Evergreen forest

All the species in this list extend into southern Nyasaland, and with the exception of *Phyllastrephus cerviniventris* none of them occur in Northern Rhodesia except in certain cases in the north. The last three on the list inhabit forest edges rather than the interior.

12. *Apaloderma (Heterotrogon) vittata*: Extends as far south in Nyasaland as Cholo and Mlanje, and in Portuguese East Africa at Namuli.

13. *Pogoniulus (Viridibucco) leucomystax/simplex*: See Nyasa/Shire List B.

14. *Indicator meliphilus*: Occurs on both sides of the Nyasa Shire Rift, even as far south as Malawi (Long, 1960-61).

15. *Phyllastrephus cerviniventris*: Extends into southern Nyasaland on both sides of the Rift, and in Northern Rhodesia as far south as Chilanga (Benson and White, 1957: 160), mainly in riparian growth.

16. *Phyllastrephus fischeri*: *P. f. placidus* occurs in Nyasaland as far south as Mlanje.

17. *Andropadus (Arizelocichla) tephrolaema*: As for the last species.

18. *Andropadus (Eurillas) virens*: Occurs in Nyasaland as far south as Cholo (Vincent, 1935).

19. *Alethe choloensis*: As far south as Cholo, and Chiperoni (Benson, 1950).

20. *Bessonornis anomala*: See Nyasa/Shire list B.

21. *Apalis chariessa*: See Nyasa/Shire list A (2).

22. *Apalis porphyrolaema*: See Nyasa/Shire list A (1).

23. *Oriolus chlorocephalus*: See Nyasa/Shire list A (2).
 24. *Nectarinia medioeris*: South in Nyasaland to the Kirk Range and Mlanje, mostly on forest edges.
 25. *Ploceus (Xanthoploceus) bertrandi*: Extends into southern Nyasaland on both sides of the Rift, almost entirely on forest edges.
 26. *Serinus (Carduelis) citrinelloides*: As for the last species, mostly in bracken growth on the edge of forest. Closely allied to *S. scotops*, see Limpopo List A (1).

Miscellaneous—mainly swamps and open grasslands

27. *Centropus cupreicaudus*: Widespread in Northern Rhodesia in swamps west of the Luangwa Rift, extending into the Caprivi, northern Bechuanaland and probably into Southern Rhodesia, but only in the extreme north-west.
 28. *Anthus leucophrys*: In Northern Rhodesia west of the Luangwa Rift, extends in open grasslands throughout Barotseland, into northern Bechuanaland (Benson and White, 1961). Recently collected on the south side of the Kafue Flats at 15°50' S., 27°05' E., and see Nyasa/Shire List A (1). It reappears in the Transvaal and the Sul do Save, but is unknown in Southern Rhodesia.
 29. *Macronyx fulleborni*: Inhabits wet grasslands in the greater part of Northern Rhodesia west of the Luangwa Rift, extending into Barotseland and plateau country in the Southern Province, but unknown any further south. In Southern Rhodesia it is replaced by the ecologically very similar *M. croceus* and *M. capensis*.
 30. *Turdoides leucopygia*: Distribution similar to the last, but extending into northern Bechuanaland. Habitat open grasslands with scattered low bushes.
 31. *Parisoma lugens*: See Nyasa/Shire list A (1).
 32. *Myrmecocichla nigra*: Inhabits dry grasslands in Northern Rhodesia west of the Luangwa Rift, extending into Barotseland and plateau country in the Southern Province.
 33. *Hirundo daurica*: This species is unknown south of the southern end of the Nyasa/Shire Rift, where it is found on both sides, on rocky hills.
 34. *Parus leucomelas*: See Nyasa Shire list A (1). In Northern Rhodesia west of the Luangwa Rift, extends south to Mazabuka.
 35. *Lagonosticta rufopicta*: See Luangwa list A (1). Recorded from the Kafue Gorge (Benson, 1959), and extends through Barotseland to the extreme north-west of Southern Rhodesia.

Exclusive of the above lists, it should be mentioned that *Cercococcyx montanus* extends in dense thickets into the extreme south of Nyasaland. The same also applies to *Merops boehmi*. McLachlan & Liversidge (1957) include the latter, but Pinto (*in litt.*) has no evidence of its occurrence in Portuguese territory south of the Zambezi, and Smithers *et al.* (1957) positively reject it for Southern Rhodesia. In any case, neither species can be formally included above, since they both occur in southern Nyasaland as low as 200 feet.

B. SUBSPECIFIC DIFFERENCES ON THE TWO SIDES OF THE VALLEY

It is also convenient to include here one species-pair, *Turdus olivaceus abyssinicus*. There are a number of very anomalous and puzzling cases in this section. It would be expected that the narrower Nyasa Shire Rift (especially the Shire section) would be of little significance compared to the Zambezi Valley. Yet one finds the same subspecies of *Tauraco persa* in eastern Southern Rhodesia and east of the Nyasa Shire Rift, but another to the west. Conversely, the same subspecies of *Cisticola aberrans* occurs in Southern Rhodesia and west of the Nyasa Shire Rift, another to the east. If the affinities of the Southern Rhodesian subspecies were always with one side or other of the Nyasa Shire Rift in those

cases in which there is a difference on the two sides of this area, the situation would be susceptible of an explanation, but this is not so. Particular attention should be drawn to the cases of *Buccanodon whytii*, *Andropadus milanjensis*, and *Apalis melanococephala*, which present even further complications. That of *Apalis thoracica*, represented by an unusually richly coloured subspecies at Mlanje and Zomba, is also most remarkable. On the other hand, the cases of *Batis capensis*, *Trochocercus albonotatus*, *Pogonocichla stellata*, and various others, in which there is one subspecies in Southern Rhodesia, another on both sides of the Nyasa Shire Rift, seem quite straightforward, according to expectation. In *Parus rufiventris*, attention may be drawn to the start of a cline in the area west of the Nyasa/Shire Rift and at Chilanga, Northern Rhodesia, but interrupted by the Valley.

1. *Tauraco persa* (—*T. corythaix*): *T. p. livingstonii* occurs in eastern Southern Rhodesia, and is separated in the Zambezi Valley below the Victoria Falls from northern populations by the competing *T. porphyreolophus*. In Northern Rhodesia and in Nyasaland west of the Nyasa Shire Rift there occurs *T. p. schalowi*, with the anomaly that to the east of the Rift *T. p. livingstonii* reappears. *T. p. schalowi* only crosses the Zambezi above the Falls at Namipini. This species inhabits evergreen forest and dense thickets. For further details, see Moreau (1958).

2. *Buccanodon whytii*: Mainly a *Brachystegia* woodland species. *B. w. irwini* occurs in the east of Southern Rhodesia, but is replaced in the north-east by *B. w. sowerbyi*, which reappears in plateau country between the Nyasa Shire and Luangwa Rifts, but is represented to the east of the former by *B. w. whytii*. The anomalous situation of two apparently distinct subspecies in Southern Rhodesia, where there is no zoogeographical barrier, with *B. w. sowerbyi* reappearing to the north of the Zambezi, requires further investigation.

3. *Motacilla capensis*: *M. c. simplicissima* is widespread in swamps in Northern Rhodesia west of the Luangwa Rift, extending into the Caprivi. But records from the Zambezi Valley are rejected by Benson (1959), while a specimen recorded by Irwin (1956) as *M. c. beirensis* has been re-examined by him and found to be a juvenile *M. aguimp*. In Southern Rhodesia the subspecies is *M. c. capensis*. For a recent revision, see Winterbottom (1959b).

4. *Andropadus milanjensis*: An evergreen forest species, represented in eastern Southern Rhodesia by *A. m. milanjensis*. On both sides of the Nyasa Shire Rift, to as far east as Cholo, Blantyre and Zomba, the easily distinguishable *A. m. olivaceiceps* (see Rand, in Mayr & Greenway, 1960) occurs. And yet at Mlanje there is the anomaly that *A. m. milanjensis* reappears, extending east to Chiperoni and Namuli. Cholo and Mlanje are little more than 20 miles apart, with intervening riparian forest, if not now destroyed in interests of agriculture.

5. *Phyllastrephus flavostriatus*: Another evergreen forest species, represented in eastern Southern Rhodesia by *P. f. flavostriatus*, in Nyasaland and Portuguese East Africa to the east of the Rift by *P. f. vincenti*, to the west by *P. f. alfredi*.

6. *Coracina caesia*: Habitat as for the last. *C. c. caesia* in eastern Southern Rhodesia, *C. c. pura* in southern Nyasaland, to the east of the Rift, also near Malawi (Long, 1959), and Chiperoni (Benson, 1950).

7. *Hyltiota australis*: A *Brachystegia* woodland species. *H. a. australis*, as in Southern Rhodesia, is recorded by Benson & White (1957) from the greater part of Northern Rhodesia. Of material in the National Museum, Bulawayo, 13 adult males from Northern Rhodesia (six from the Southern Province, three from the Northern Province, four from the North-Western Province) are rather more intensely black above, less intensely washed with buff below, than in 17 from Southern Rhodesia. No such analogous differences are discernible in females, of which four have been available from Northern Rhodesia (two from the Southern Province, one from the Central Province, one from the North-Western Province), and 14 from Southern Rhodesia. Reference variation in the pattern of the outer pair of tail-feathers,

discussed by White (1957) and Hall (1960), the specimens from the Northern and North-Western Provinces lack any white. The remainder all show a variable amount of white. Birds from the southern part of Northern Rhodesia may be referable to *H. a. inornata*, described from east of the Luangwa Rift (no specimens from that area have been available), but in any case they are not identical with *H. a. australis*.

8. *Batis capensis*: Habitat evergreen forest. *B. c. erythrophthalma* in eastern Southern Rhodesia, *B. c. dimorpha* in southern Nyasaland and Portuguese territory on both sides of the Rift.

9. *Trochocercus albonotatus*: Habitat as for the last. *T. a. swynnertoni* in eastern Southern Rhodesia, *T. a. albonotatus* in southern Nyasaland and Portuguese territory on both sides of the Rift.

10. *Turdus olivaceus abyssinicus*: *T. o. swynnertoni* occurs in evergreen forest in eastern Southern Rhodesia, being replaced in southern Nyasaland on both sides of the Rift by the analogous and closely allied *T. abyssinicus milanensis* (regarded as a different species, following Chapin, 1953). *T. olivaceus* reappears in the north of Northern Rhodesia, west of the Luangwa Rift, as *T. o. stormsi*.

11. *Thammodia cinnamomeiventris*: A rock-frequenting species, represented south of the Zambezi by *T. c. cinnamomeiventris*, to the north by *T. c. subrufipennis*. The occurrence of the former at the Victoria Falls (Benson & White, 1957) has not so far been substantiated.

12. *Pogonocichla stellata*: An evergreen forest species. *P. s. transvaalensis* in eastern Southern Rhodesia, *P. s. orientalis* on both sides of the Rift in southern Nyasaland and Portuguese East Africa. See especially Moreau (1951).

13. *Bradypterus baboecala*: A swamp-dweller, represented by *B. b. baboecala* in Southern Rhodesia, by *B. b. moreaui* in Nyasaland and eastern Northern Rhodesia. Western Northern Rhodesia, the Caprivi and northern Bechuanaland are inhabited by *B. b. msiri*. See White (1960d).

14. *Bradypterus barratti*: *B. b. priesti* occurs in eastern Southern Rhodesia, in and around the edges of evergreen forest. It is replaced in southern Nyasaland by *B. b. granti* (*Sathrocercus mariae* in Benson, 1953, the nomenclature here adopted being that of White, 1960d).

15. *Apalis thoracica*: *A. t. whitei* of southern Nyasaland west of the Nyasa Shire Rift is considered by White (1960c) a synonym of *A. t. arnoldi* of eastern Southern Rhodesia. Yet on the east of the Rift there is the very distinct *A. t. flavigularis*. See further under Nyasa Shire list B.

16. *Apalis melanocephala*: In evergreen forest in the highlands of eastern Southern Rhodesia there occurs the very distinct *A. (m.) chirindensis*. Near the confluence of the Haroni and Lusitu Rivers, at the southern end of the Chimanimani Mts., *A. m. lightoni* occurs, also found at Beira, and again in southern Nyasaland on the east of the Rift from Blantyre northwards, but with intervening forests at Mlanje and Cholo occupied by *A. m. fuliginosa*.

17. *Eremomela scotops*: Frequents mainly Brachystegia woodland, generally rare or absent from low levels. In Southern Rhodesia it is represented by *E. s. scotops*, reappearing on the eastern side of the Nyasa Shire Rift, except at Matindi, north of Blantyre, where it is replaced by *E. s. pulchra*. *E. s. pulchra* is the form west of the Rift, and in Northern Rhodesia, intergrading with *E. s. scotops* in north-eastern Matabeleland (Smithers *et al.*, 1959), the Zambezi above the Victoria Falls forming no barrier.

18. *Camaroptera stierlingi*: Mainly a Brachystegia woodland species. According to Irwin (1960), Southern Rhodesia is inhabited by *C. s. irwini*, extending across the Zambezi above the Victoria Falls into the Livingstone and Kalomo Districts of Northern Rhodesia (recent specimens are also available from the Choma District), but is replaced further north by *C. s. butoni*. *C. s. irwini* reappears in plateau country between the Luangwa and Nyasa/Shire Rifts, while east of the latter *C. s. stierlingi* occurs. Irwin records *C. s. butoni* from the

Gwembe Valley. Actually the specimen on which this is based (see also Benson, 1960a) was collected on the lip of the escarpment at an altitude of 4,000 feet. There appear to be no records from the Zambezi Valley proper, which makes it difficult to explain the reappearance of *C. s. irwini* in eastern Northern Rhodesia and western Nyasaland. However, it may be that it extends across the valley sparsely, and has so far been overlooked. Benson (1953) gives a few records of the species from within the Nyasa/Shire Rift.

19. *Cisticola brunnescens*: In Mashonaland represented in wet short grasslands by a population regarded as intermediate between *C. b. egregia* and *C. b. cinnamomea*. Northern Rhodesia west of the Luangwa Rift to as far south as Broken Hill (Benson, 1959), the Busanga Swamp (recent specimens) and Lueke are inhabited by *C. b. cinnamomea*.

20. *Cisticola lais*: In montane short grasslands in eastern Southern Rhodesia, *C. l. mashona*; replaced on both sides of the Nyasa Shire Rift in southern Nyasaland by *C. l. semifasciata*.

21. *Cisticola tinniens*: *C. t. tinniens* occurs in swamps in Southern Rhodesia, while *C. t. shiwa* extends south in Northern Rhodesia to the Mkushi River (Benson, 1959).

22. *Cisticola aberrans*: *C. a. nyika* is widespread in scattered rocky localities, usually in *Brachystegia* woodland, in Southern and Northern Rhodesia, and Nyasaland west of the Nyasa Shire Rift, but is replaced to the east by *C. a. lurio* (regarded by White, 1960b, as conspecific with *C. aberrans*).

23. *Lanius collaris*: Open grassy areas with scattered bushes above 3,000 feet in Southern Rhodesia are inhabited by *L. c. subcoronatus* and *L. c. predator*. In Northern Rhodesia the species is represented by *L. c. capelli*, and is generally absent from lower levels (Benson, 1959). This subspecies extends at least as far south as the Choma and Sesheke Districts (Benson, *op. cit.* and 1960b). For the position in Nyasaland, see Nyasa/Shire Rift list B.

24. *Malaconotus olivaceus*: An evergreen forest species, represented by *M. o. makawa* in eastern Southern Rhodesia and southern Nyasaland west of the Nyasa/Shire Rift, but by *M. o. bertrandi* to the east.

25. *Parus rufiventris*: A very anomalous case. *P. r. pallidiventris* occurs in north-eastern Southern Rhodesia south to Mt. Selinda, in *Brachystegia* woodland. It reappears to the east of the Nyasa Shire Rift, but is represented to the west by *P. r. masukuensis*, except that from Zobue, *P. r. pallidiventris* has been recorded (Vincent, 1935), while specimens from Fort Jameson incline towards the latter. The Zobue specimen has been re-examined by Mrs. B. P. Hall, from whose report however it is evidently only slightly paler rufous on the belly than in specimens of *P. r. masukuensis*, and accordingly closer to that form, while a specimen from Pirilongwe is evidently intermediate. In Northern Rhodesia west of the Luangwa Rift, *P. r. masukuensis* ranges south to near the lip of the escarpment at Chilanga, though a series of eight specimens from this locality actually show slight signs of intergradation with *P. r. pallidiventris*, being rather paler on the belly than in *P. r. masukuensis*.

26. *Nectarinia chalybea*: Mainly a *Brachystegia* woodland species. The populations of Southern and Northern Rhodesia are quite easily distinguishable, the former as *N. c. bractiata*, the latter as *N. c. intermedia* (Benson & White, 1957: 162). *N. c. intermedia* extends as far south as the Kalomo District (Benson, 1959) and has recently been collected in the Choma District on the tip of the escarpment at 17°00' S, 27°20' E. According to Macdonald (1958), *N. c. bractiata* is a synonym of *N. c. manoensis*, which is the form in southern Nyasaland. Macdonald gives the Luangwa as the dividing line between *N. c. intermedia* and *N. c. bractiata*, whereas Benson & White place all Northern Rhodesian birds with *N. c. intermedia*. The problem requires further investigation, but it appears that the Zambezi Valley acts as a subspecific barrier at least in the sector between the Victoria Falls and Feira, but not so further east, even though there is no evidence of the occurrence of the species lower than 2,500 feet.

27. *Nectarinia olivacea*: An evergreen forest species, represented in the highlands of eastern Southern Rhodesia by *N. o. sclateri* and in southern Nyasaland on both sides of the Nyasa Shire Rift by *N. o. alfredi*. Intermediates between *N. o. alfredi* and *N. o. lowei* have recently been obtained near Lusaka.

28. *Antheptes longuemarei*: A Brachystegia woodland species, represented in northern Mashonaland and eastern Southern Rhodesia by *A. l. nyassae*. In Northern Rhodesia and Nyasaland west of the Nyasa Shire Rift the form is *A. l. angolensis*, but to the east *A. l. nyassae* reappears. In Northern Rhodesia *A. l. angolensis* has recently been obtained on the very lip of the Zambezi escarpment in the Choma District at 17 00' S., 27 20' E.

29. *Serinus gularis*: A Brachystegia woodland species; *S. g. gularis* in Southern Rhodesia, *S. g. reichardi* in Nyasaland and in Northern Rhodesia, where it occurs as far south as the Kalomo District (Benson, 1959). The statement by Vincent (1952) that *S. g. reichardi* occurs in the Lower Zambezi Valley cannot be accepted (Clancey, 1960).

30. *Fringillaria capensis*: *F. c. plowesi* inhabits rocky localities in Southern Rhodesia, and is replaced in Northern Rhodesia east of the Luangwa Rift and in Nyasaland and Portuguese East Africa by *F. c. vincenti*. On the Chimanimani Mts. there occurs a more distantly related form, *F. c. smithersii*. See Irwin (1958).

Although *Centropus t. grillii* is recorded for Northern Rhodesia and Nyasaland, and *C. t. wahlbergi* for Southern Rhodesia, Irwin (in MS for *Bull. Brit. Orn. Cl.*) has shown that they are synonymous, so that this species cannot be included above.

Although 30 instances are given above of the subspecific differences between the two sides of the Zambezi Valley (contrarily in some cases the same subspecies as in Southern Rhodesia occurs in part of the area to the north), it is particularly noteworthy that there is no less a number of instances of no such differentiation anywhere on either side, even though there is no evidence at all of any gene-flow. They may be briefly mentioned by rough, somewhat arbitrary ecological categories, giving subspecific names for those (the great majority) in which trinomials can be supported:—

Brachystegia woodland: *Muscicapa adusta subadusta*, *Parus griseiventris*, *Salpornis spilonota salvadorii*, *Emberiza cabanisi orientalis* (synonym *E. c. cognominata*).

Evergreen forest: *Accipiter r. rufiventris*, *Columba a. arquatrix*, *Aplopelia l. larvata*, *Bycanistes brevis*, *Turdus g. gurneyi*, *Phylloscopus ruficapilla johnstoni*, *Malacothraupis nigrifrons sandgrounderi* (see Moreau & Southern 1958), *Hypargos n. nitidulus*, *Cryptospiza reichenovii australis* (southern specimens rather larger, Smithers *et al.*, 1959).

Largely forest edges, secondary bracken growth & c.: *Cossypha caffra iolaema*, *Chloropeta n. natalensis*, *Cisticola cantans munzneri*, *Nectarinia kilimensis arturi*, *Estrilda melanotis kilimenis*.

Montane short grasslands: *Coturnix coturnix africana*, *Sarothrura affinis antonii* (for Southern Rhodesia records for these last two, see Smithers *et al.*, 1959). *Cisticola a. ayresii* (only again in extreme north of Northern Rhodesia and Nyasaland), *Hirundo atrocaerulea*.

Wet short grasslands: *Schoenicola platyura brevirostris* (see White, 1960d), *Euplectes m. macrourus*, *Ortygospiza l. locustella*.

Dry short grasslands: *Turnix nana luciana*, *Mirafra africana transvaalensis* (see Rand, in Mayr & Greenway, 1960).

The following must also be included:—*Bubo c. capensis*, habitat uncertain (probable in Southern Rhodesia, Smithers *et al.*, 1959); *Motacilla clara torrentium*, perennial rivers and streams; *Anthus lineiventris*, rocks.

THE LUANGWA RIFT

The Luangwa River rises in the Mafinga Mts., on the Northern Rhodesia Nyasaland border. It falls almost immediately into a wide valley floor. The altitude near the head

of the river in the Isoka District is almost 3,000 feet, and it drops gently to below 1,000 feet at its confluence with the Zambezi, some 400 miles to the south-west. The valley is as much as 40 miles across in part of the Mpika, Lundazi and Fort Jameson Districts, where the predominant vegetation is Mopane woodland, intersected by alluvial *Acacia* growth. It is enclosed by a high escarpment wall, attaining in places an altitude of near 6,000 feet down the western side from the Mpika District southwards. There is also a steep escarpment on the eastern side in the Isoka District down to the neighbourhood of the Ruwumbu, but below this point the eastern escarpment consists merely of a zone of stony hills gradually rising towards the plateau, at a general level of between 3,000 and 4,000 feet. At about 14° 15' S., the valley practically disappears, foot-hills on both sides closing with the river. Mention should also be made of the subsidiary Lukusashi and Lunsemfwa troughs (the latter also known as the Luano Valley), more than 10 miles across in places, with vegetation akin to that in the Luangwa Valley. But not enough is known about the avifauna in their immediate vicinity for it to be possible to decide whether they act as barriers in any way, and so they are not dealt with below. Probably, like the Sabi, their influence is insignificant.

The annual rainfall in the Rift as a whole is less than in the surrounding plateau country, averaging 24 to 32 inches, compared to 32 to 40 inches (see map in Brelsford, 1960). By contrast to the Mopane woodland of the Rift itself, the predominant vegetation of the plateau country is *Brachystegia* woodland. The foregoing brief description is taken from Trapnell (1953), and the map in Trapnell *et al.* (1948).

In the Rift itself various birds are widespread which are unknown in the surrounding plateau country. Examples are *Pterocles bicinctus*, *Tockus erythrorhynchus*, *Lamprolornis mevesii* and *Plocepasser mahali*. The instances which follow of the Rift acting as a distributional barrier are derived mainly from Benson & White (1957) and from Benson (1953). Where additional information is available, the authority is quoted. In none of these instances does there seem to be any ecological reason why a species should not be present on both sides of the Rift, except in the case of a species-pair, such as *Macronyx fulleborni* and *M. croceus*, whose ecological requirements are very similar, and therefore replace each other. It is true that in the north of Northern Rhodesia there are forests with a damp, peaty floor, locally known as "mushitu" (Benson & White, 1957: XIII), such as are not found to the east of the Rift. But all the evergreen forest dwelling species included below in list A (1) can also exist in riparian evergreen forest, of which there is no lack to the east of the Rift.

Certain essentially montane species, found to the east of the rift in such localities as Dedza, and the Vipya and the Nyika plateaux, in Nyasaland, rising to 7,000 feet or even higher, are not included in the lists of examples below. It is true that some of them reappear in western Angola (Heinrich, 1958; Hall, 1960), but they are unknown in the highlands in the Serenje and Mpika Districts on the west of the Rift, presumably because these do not rise high enough. Examples of such reappearances are *Apaloderma (Heterotrogon) vittata*, *Melaenornis chocolatina* (= *Dioptrornis chocolatina brunnea*), *Turdus gurneyi*, *Bradypterus barratti* (= *B. mariae*), *Cisticola lais*, *Nectarinia kilimensis* and *Cryptospiza reichenovii*.

In the examples below, the number of species restricted to the western side of the Rift (list A (1)) greatly exceeds that of those restricted to the eastern side (list A (2)). All in the former category extend across from western Angola, and it is also noteworthy that in the majority of cases this is even without any subspecific variation. It is only in the case of examples 7, 9, 12, 13, 14, 16 and 19 that there is such a difference. Another striking point is that although the predominant vegetation in this extensive area is *Brachystegia* woodland, only two (examples 10 and 17) are associated with this habitat. The explanation of this may be that it is easier for such species to gain access to the opposite side of the Rift, around the northern end, or even through the Mopane woodland in the Rift itself (thus Benson & White, 1957, give odd records of such typically *Brachystegia* species as *Caprimulgus pectoralis*, and

Salpornis spilonota from the Luangwa, outside their normal habitat). There are many rather strictly *Brachystegia*-frequenting species common to the two sides of the Rift, but unknown within it. To list them would occupy an undue amount of space, but perusal of Benson & White (1957) shows the number to be approximately thirty.

In the following list, it should be noted that Musense is at the top of the western escarpment of the Rift, in the Serenje District, and at 13° 15' S., 31° 05' E. (not 30° 05' E., as given by Benson *et al.*, 1961). Any specimens mentioned as recently collected are in the National Museum, Bulawayo.

A. SPECIES WHOSE RANGE IS LARGELY OR COMPLETELY RESTRICTED BY THE RIFT.

(1) *Occurring entirely (or almost so) only on the western side, typically ranging through the north of Northern Rhodesia and the southern Congo from western Angola*

1. *Centropus cupreicaudus*: A swamp-dweller, only certainly known further east at the mouth of the Songwe River, at the north end of Lake Nyasa. Admittedly there is an old specimen from South Angoniland (the present Ncheu and Dedza Districts of Nyasaland), but as this record has not since been corroborated the specimen may well have been mislabelled. There is no geographical variation except that the Songwe birds are rather small (Traylor, 1960—it is considered that *C. c. songweensis* is a form of *C. cupreicaudus*, and that this is not conspecific with *C. monachus*).

2. *Musophaga rossae*: This monotypic species approaches the western escarpment at about 14° 30' northwards. It is unknown in Nyasaland, and at the north end of the Rift is only known as far east as Old Fife. It inhabits evergreen forest.

3. *Lybius minor*: *L. m. macclouniei* extends from western Angola eastwards, reaching the escarpment at 14° northwards. It does extend around the north end of the Rift, but only into the Karonga District of Nyasaland. Habitat as for the last species.

4. *Motacilla capensis*: *M. c. simplicissima* is widespread in Angola, and in Northern Rhodesia west of the Rift, being found in swamps as far east as Lusiwash and Shiwa Ng'andu. It is recorded by Winterbottom (1959b) from Nyasaland, but no supporting evidence for this has been traced.

5. *Turdoides leucopygia*: *T. l. hartlaubii* is widespread in Angola, and in Northern Rhodesia west of the Rift, in open grasslands with scattered low bushes.

6. *Chlorocichla flavicollis*: *C. f. flavigula* is widespread in the north of Northern Rhodesia. It reaches the western side of the Rift between Isoka and Serenje, and inhabits evergreen forest.

7. *Campephaga quiscalina*: *C. q. martini* is known from scattered localities in the north of Northern Rhodesia, in evergreen forest. It is unrecorded any further east than Kasama and the Mlembo River, in the Serenje District.

8. *Myrmecocichla nigra*: This monotype species is widespread in Northern Rhodesia west of the Rift. Although Benson & White (1957) give its habitat as large dry plains, such as are lacking east of the Rift, it does also inhabit the edges of small dambos, which are in fact found to the east.

9. *Cossypha bocagei*: *C. b. chapini* extends across the north of Northern Rhodesia in evergreen forest, to near the western escarpment of the Rift at Danger Hill, and at Musense (Benson *et al.*, 1961).

10. *Eremomela atricollis*: This monotypic, *Brachystegia* woodland frequenting species ranges through the north of Northern Rhodesia to near the western side of the Rift at Mpika, Chinsali (Benson, 1959) and Serenje (Benson *et al.*, 1961).

11. *Cisticola brunnesens*: *C. b. cinnamomea* ranges from western Angola across the north of Northern Rhodesia, as far as the Serenje, Mpika and Chinsali District, in wet grasslands.

The same subspecies does in fact reappear on the north-east side of the Nyasa/Shire Rift, at Njombe (Lynes, 1934).

12. *Cisticola pipiens*; 13. *C. tinniens*; 14. *C. robusta*: All three species are widespread in the north of Northern Rhodesia (*C. pipiens* extending in the west south to northern Bechuanaland). The swamp-dwelling *C. p. congo* extends east to Mbesuma, thence south-west to the Mkushi River (Benson, 1959). *C. t. shiwae*, of very similar habitat, ranges east to Shiwa Ng'andu, Lusiwash, and also the Mkushi River (Benson, 1959), while *C. r. awemba* of wet grass lands, occurs as far east as Kasama and Serenje.

15. *Dicrurus ludwigii*: *D. l. ludwigii* ranges in evergreen forest through the north of Northern Rhodesia to the Serenje and Mpika Districts. This is considered a fair example for inclusion even though the same subspecies reappears in the south of the Nyasa/Shire Rift, and in the highlands to the east thereof. There is apparently perfectly suitable habitat in the intervening area.

16. *Ploceus bicolor*: *P. b. kigomaensis* ranges in evergreen forest through the north of Northern Rhodesia to the western escarpment at Muzyabama and Danger Hill. The species is unknown further east in Northern Rhodesia, but is represented in southern Nyasaland by *P. b. stictifrons*. This case is somewhat analogous to that of *Dicrurus ludwigii*.

17. *Ploceus (Phormoplectes) angolensis*: This apparently monotypic, *Brachystegia* woodland frequenting species ranges east to the Kondolilo Falls, in the Serenje District (Benson *et al.*, 1961), and has more recently been seen by Benson at the top of the escarpment at Musene. On the east side of the Rift there occurs the very differently coloured *P. olivaceiceps* (see list A (2)).

18. *Euplectes hartlaubi*: *E. h. hartlaubi* extends in dambos to the west of the Rift, between Broken Hill and Isoka. Another very distinct form, perhaps better regarded as a distinct species, *E. psammochromius*, occurs to the east, on the Nyika, and again at Njombe (Lynes, 1934).

19. *Ortygospiza atricollis*: Widespread in various subspecies, extending even south to the Cape Province. But in Northern Rhodesia only found on plains and dambos to the west of the Rift, though also occurring in the littoral at the north end of Lake Nyasa.

20. *Lagonosticta rufopicta*: *L. r. nitidula* ranges from northern Angola to the west side of the Rift, usually being found in small thickets.

21. *Lagonosticta caerulescens*: *L. c. perreini* extends mainly in evergreen forest to the western escarpment in the Mpika and Lundazi Districts, only extending around the north end of the Rift to Muyombe, in the east of the Isoka District. The species is unrepresented further east except by an isolated record of *L. c. incana* from Mbamba Bay, in the north-east littoral of Lake Nyasa (Meise, 1937), and is not otherwise known north of the extreme south of Nyasaland.

22. *Estrilda paludicola*: *E. p. guellensis* is found in dambos to as far east as the Mpika and Serenje Districts west of the escarpment.

(2) Occurring practically only on the eastern side, essentially generally of an eastern distribution.

1. *Bycanistes brevis*: This species is unknown west of the Rift. To the east it occurs in several localities in highland evergreen forest in Nyasaland, where it is probably not more general through competition with *B. bucinator*.

2. *Pogoniulus (Viridibucco) leucomystax*: This monotypic species is widespread in evergreen forest in the highlands of Nyasaland west of the Nyasa/Shire Rift, but is unknown to the west of the Luangwa Rift.

3. *Pogonochila stellata*: An evergreen forest species, mainly at higher altitudes. Common in Nyasaland west of the Nyasa Shire Rift, and in Northern Rhodesia occurs to

the east of the Luangwa Rift on the Nyika and the Mukutu Mts., and at the top end of the Rift at Old Fife.

4. *Cisticola cantans*: This species is unknown west of the Rift. *C. c. munzueri* occurs on higher ground to the east, to as low as Fort Jameson, mainly in bracken growth.

5. *Hirundo daurica*: Included in the range of *H. d. emini* is the rocky, mountainous country between the Luangwa and Nyasa Shire Rifts. To the west, it is unknown in apparently very suitable country in the Mpika and Serenje Districts, even though it does occur in the Abercorn District, and the Upemba National Park (Verheyen, 1953).

6. *Ploceus (Phormoplectes) olivaceiceps*: This occurs in Brachystegia woodland at higher levels on the east side of the Rift, in Nyasaland, extending north to nearly 11°. See also list A (1) above.

7. *Serinus citrinelloides*: *S. c. hypostictus* occurs on higher ground to the east of the Rift, typically in bracken growth on the edge of evergreen forest, and is found as low as Fort Jameson. The species is only known further west in Northern Rhodesia at Abercorn, where *S. c. frontalis* occurs.

8. *Fringillaria capensis*: *F. c. vincenti* extends north to the south of the Mzimba District, on rocky hills, but the species is unknown in similar country on the western escarpment of the Rift.

It might be thought that *Aquila verreauxi*, widespread in rocky localities in Nyasaland, and only certainly recorded from Northern Rhodesia from Nyanje, to the east of the Rift, is an example. But as it has recently been recorded by Benson (1959) from the Luano escarpment it is excluded.

B. SPECIES-PAIRS SEPARATED BY THE RIFT, OR SPECIES SHOWING SUBSPECIFIC DIFFERENCES ON THE TWO SIDES

Ploceus (Phormoplectes) angolensis and *olivaceiceps* have been dealt with above. They could conceivably have been included here, but the colour-differences are so great that this seems hardly justified.

1. *Pogoniulus bilineatus*: *P. b. mfambiri* ranges in evergreen forest from eastern Angola across the north of Northern Rhodesia to the western escarpment of the Rift at Danger Hill. *P. b. bilineatus* has been recorded in the highlands of Nyasaland west of the Nyasa Shire Rift from the Vipya and Nyankhowa. That it is not more general in that area may be due to competition with *P. leucomystax*.

2. *Macronyx fulleborni croceus*: *M. f. ascensi* extends across from western Angola, and is widespread in Northern Rhodesia west of the Rift. Its range approaches very closely that of *M. croceus* at the north end, in the Isoka District, this latter species being widespread in Nyasaland, and in Northern Rhodesia on the east of the Rift. They both inhabit moist, spongy grasslands, and their ranges as a whole are largely mutually exclusive.

3. *Phyllastrephus fischeri*: *P. f. cabanisi* ranges in evergreen forest from western Angola across the north of Northern Rhodesia to the western escarpment of the Rift between Mkushi and Isoka. *P. f. placidus* occurs in certain areas of forest, from Thambani to the Masuku Mts., between the Luangwa and Nyasa/Shire Rifts.

4. *Turdus olivaceus abyssinicus*: *T. o. stormsi* is widespread in the north of Northern Rhodesia, in evergreen forest, but is unknown east of Danger Hill, and the western escarpment of the Rift at Musense (recent sight-record by Benson). It is replaced in scattered localities at high altitudes to the east of the Rift by *T. a. nyikae* to as far south as about 11°, and by *T. a. milanienensis* at Dedza. *T. olivaceus* and *T. abyssinicus* have often been regarded as conspecific, but overlap elsewhere (Chapin, 1953).

5. *Phylloscopus ruficapilla*: The richly coloured western *P. r. laurae* and *P. r. eustacei*

were united by White (1960d) with *P. ruficapilla*. *P. r. eustacei* ranges in evergreen forest east to the escarpment of the Rift at Danger Hill. and Musense (Benson, *et al.*, 1961). *P. r. johnstoni* is found in the highlands of Nyasaland west of Lake Nyasa at Nchisi and north of about 11°.

6. *Camaroptera stierlingi*: According to Irwin (1960), *C. s. buttoni* ranges from the Mpika District south-west to Gwembe, Mankoya and Sesheke. The species inhabits *Brachystegia* woodland, and is unknown in the Luangwa. To the east thereof *C. s. buttoni* is replaced by *C. s. irwini*.

7. *Cisticola natalensis*: *C. n. katanga* is widespread west of the Rift, in open grasslands. It ranges south to Monze, while specimens from Kasusu, in the Kalomo District, are nearer *C. n. holubi* (Benson, 1959). Recent specimens from near Choma show a slight tendency towards *C. n. holubi*. *C. n. katanga* only ranges around the north end of the Rift to as far as Fort Hill, Nyasaland. It is otherwise replaced to the east by *C. n. natalensis*, and is unknown in the Luangwa itself.

8. *Malacotus nigrifrons*: *M. n. manningi* ranges through the north of Northern Rhodesia to Danger Hill. On the east of the Rift, *M. n. nigrifrons* occurs on the Nyika (see also Nyasa/Shire list).

9. *Pirenestes ostrinus minor*: *P. o. frommi* is known from a few localities in the north of Northern Rhodesia, in evergreen forest, to as far east as the western escarpment of the Rift in the Lundazi and Mpika Districts. *P. minor* is known from scattered localities in the more humid parts of Nyasaland, in bracken growth on the edge of evergreen forest, including, to the west of the Nyasa Shire Rift, the Vipya Plateau, and Furancungo (Vincent, 1936). A larger heavier billed form, named *P. vincenti* by Benson (1955b), probably a mere variant of *P. minor*, has been recorded from Furancungo. It serves to emphasise the close relationship of *P. minor* to *P. ostrinus*.

Anthus c. caffer is known from the Mpika District by two specimens, and *A. c. mzimbaensis* by one specimen from the Mzimba District, to the east of the Rift (Benson, 1955a). In view of the paucity of specimens, this case is not formally included above.

Anthoscopus caroli robertsi is recorded from the east of the Rift, intermediates between *A. c. rhodesiae* and *A. c. caroli* from the Mpika District to the west, and also in the Serenje District (Benson *et al.*, 1961). Actually such intermediates can be as well placed with *A. c. winterbottomi*, and a recent examination of material in the National Museum, Bulawayo shows the differences between this form and *A. c. robertsi* to be inappreciable. Consequently this case is not included above.

Also, it might be thought that an example is afforded by *Nectarinia olivacea alfredi* (on the east) and *N. o. lowei* (on the west). But recently intermediate specimens have been collected near Lusaka, where typical *N. o. lowei* would have been expected.

C. SOME MISCELLANEOUS INSTANCES, NOT FITTING INTO CATEGORIES A OR B ABOVE

1. *Cisticola galactotes*: *C. g. galactotes* (synonym *C. g. luapula* White, *in litt.*) is widespread in swamps in Northern Rhodesia west of the Rift. The species is unknown in the Rift itself, where there is little or no suitable habitat, but this does not explain its absence also from plateau country to the east. It occurs throughout the Nyasa/Shire Rift (*C. g. suahelica*).

2. *Cisticola chiniana*: *C. c. fortis* ranges from western Angola through the north of Northern Rhodesia, in secondary Acacia and *Brachystegia* scrub, to the western escarpment in the Mpika and Serenje Districts. In the Rift itself it is replaced by *C. c. procera* ranging eastwards into Nyasaland (White, 1960a).

3. *Sphenoeacus (Melocichla) mentalis*: West of the Rift, in rank grass growth near streams, there occurs *S. m. mentalis*, ranging east from western Angola. In the Rift itself north of about 13° 15', there occurs the paler *S. m. luangwae*, extending east to Fort Jameson (corrobo-

rated by several recent specimens). *S. m. orientalis* probably ranges throughout Nyasaland. For nomenclature as above, see White (1960d).

4. *Euplectes axillaris*: *E. a. bocagei* extends from western Angola to swamps west of the Rift, in the Northern Province. The species reappears in the Nyasa/Shire Rift, *E. a. axillaris* in the south, probably nearer *E. a. phoeniceus* in the north. This example resembles that of *Cisticola galactotes*.

Benson & White (1957) indicate that the Muchinga (the western) escarpment to the Rift is the dividing line between *Numida meleagris marungensis* and *N. m. mitrata*. But specimens recently collected at Musense, at the top of the escarpment, are intermediate. Furthermore, they record *N. m. mitrata* from Mbesuma, and Benson (1959) likewise from Isoka, both localities being to the west.

THE NYASA/SHIRE RIFT

The Nyasa/Shire Rift extends through the length of Nyasaland from north to south. The floor of the Nyasa Rift is in part occupied by the Lake Nyasa, at 1,550 feet, but in places over 2,200 feet deep, so that parts of the floor are more than 700 feet below sea-level. The Shire Rift is traversed by the Shire River, forming an intermittent outlet from Lake Nyasa to the lower Zambezi, almost at sea-level. The greater part of the Rift is bounded on either side by plateau country mainly between 3,000 and 4,000 feet in altitude, in which the predominant vegetation is *Brachystegia* woodland. This plateau country is surmounted by a number of small plateaux, attaining elevations usually of 6,000 to 7,000 feet, but sometimes exceeding 8,000 feet. Such plateaux are characterised by undulating short grasslands and evergreen forest often not merely riparian in extent. In the Nyasa section, the Rift is as much as 60 miles across, and the lake itself in places almost as much, but in the Shire section not much over 20 miles wide in the Blantyre District, and the escarpment on both sides is more gradual than further north.

In the Rift itself the rainfall average is generally higher than in the Luangwa Rift (see rainfall map in Brelsford, 1960), and the figures are only comparable from the south end of Lake Nyasa southward. In the Kotakota and Chinteché Districts, and at the north end of the lake, the annual average is everywhere at least 56 inches. In contrast to the Luangwa, too, Mopane woodland is by no means so prevalent, and in the lake littoral is unknown north of Ntakataka, in the Dedza District Acacia and palm growth (Benson, 1953: 6) is more in evidence, while from Salima northwards *Brachystegia* woodlands occur. Between Chinteché and Nkata Bay, where the annual rainfall average is as much as 80 inches, evergreen forest is even prevalent in some places. Between Nkata Bay and Livingstonia the escarpment extends for the most part directly down to the lake, and there is very little flat littoral country. By reason of the ecological conditions some species of birds which are normally only found at higher elevations extend to the level of Lake Nyasa in the Kota-kota and Chinteché Districts.

As might be expected, by contrast to the Luangwa, *Tockus erythrorhynchus*, *Lamprolornis mevesii* and *Plocepasser mahali* are by no means so generally distributed, and do not extend far north of the south end of Lake Nyasa, while *Pterocles bicinctus* is only known from the south-west of the Chikwawa District. Another rather typically semi-arid species extending to the south end of Lake Nyasa is *Amadina fasciata*.

The instances which follow of the Nyasa/Shire Rift acting as a barrier are derived so far as Nyasaland is concerned from Benson (1953). For northern Portuguese East Africa, Vincent (1933-6) has been more especially useful, while Chiperoni records are by Benson (1950). As with the Luangwa, the number of species confined to the west side of the Rift considerably exceeds those confined to the east side.

Two complications should be mentioned. See Dixey (1931), west of Fort Johnston there is high ground culminating in the peak of Piri-longwe, at a height of over 5,000 feet,

while further west the altitude drops to below 2,000 feet before rising again. From the lists below, the presence of *Sylvietta ruficapilla* and *Cisticola aberrans nyika* suggests a western affinity, but that of *Anthreptes longuemarei nyassae* an eastern. Also, west of the Shire River at Port Herald there is isolated high ground rising to over 3,000 feet (Malawi Hill). But the presence of *Buccanodon leucotis*, *Phyllastrephus flavostriatus vincenti*, *Coracina caesia* and *Camaroptera s. stierlingi* suggests eastern rather than western affinities. On the other hand, the presence of *B. molitor* suggests the latter.

A. SPECIES WHOSE RANGE IS ALMOST COMPLETELY RESTRICTED BY THE RIFT

(1) Occurring mainly on the western side

1. *Lybius leucomelas* (= *Tricholaema diadematum*): *L. l. frontatus* ranges south to Kasungu, and to Chadiza, in the Fort Jameson District (Benson, 1958), in *Brachystegia* woodland. It is unknown east of the Rift.

2. *Anthus leucophrys*; 3. *Anthus vaalensis*: Neither species is known to the east of the Rift, and the only record from within the Rift is of *A. leucophrys* from near the mouth of the River Songwe, at the north end of Lake Nyasa. To the west, *A. leucophrys* extends as far south as the River Bua, *A. vaalensis* to Ncheu.

4. *Parisoma lugens*: On the west, extends south to 15° 30', but on the east unknown south of the Matengo Highlands (Sassi & Zimmer, 1941). This species is largely confined to trees of *Acacia abyssinica* (= *A. woodii* in Benson, 1953), of which there is no lack in southern Nyasaland to the east of the Rift.

5. *Melaenornis (Dioptrornis) chocolatina*: On the west, on the edge of montane evergreen forest to as far south as Dedza, but on the east unknown south of Njombe (Lynes, 1934).

6. *Muscicapa (Myopornis) boehmi*: Ranges in *Brachystegia* woodland on the west side south to Kapiriuta. Unknown to the east, though known on the east side of Lake Tanganyika as far north as Tabora.

7. *Elminia albicauda* (= *Erannornis longicauda*): On the west south in *Brachystegia* woodland and the edge of riparian forest to Zobue, but on the east unknown south of the Matengo Highlands (Sassi & Zimmer, 1941).

8. *Turdus litsipsirupa*: On the west, south in *Brachystegia* woodland to Ncheu; on the east known only from Njombe (Sassi & Zimmer, 1941).

9. *Erythropygia barbata*: Ranges south, mostly in *Brachystegia* woodland, to the River Bua and Fort Jameson, on the western side. In the Rift itself, occurs in this type of habitat near Kota-kota and Karonga. Only the closely related *E. quadrivirgata* occurs to the east of the Rift (and in the Rift itself), but probably never in so open a type of habitat as *Brachystegia*.

10. *Apalis porphyrolaema* (= *A. bamendae*): Occurs on the west south to about 14° 30', in highland evergreen forest, but unknown on the east side south of Njombe (Lynes, 1934).

11. *Sylvietta ruficapilla*: General on the west, in *Brachystegia* woodland, and also known from Piri-longwe. Although it extends sparingly to the littoral of Lake Nyasa at Kota-kota and Karonga, unknown to the east of the Rift.

12. *Cisticola rufilata*: Only on the west side, in scattered secondary *Brachystegia* scrub localities from the Ncheu District to Mzimba.

13. *Hirundo dimidiata*: Only on the west side, sparsely throughout from Ncheu northwards, in clearings in *Brachystegia* woodland.

14. *Hirundo semirufa*: Recorded from the Ncheu and Dedza Districts, and from Fort Jameson, associated with moist, spongy grasslands. Probably general west of the Rift, but no records from the east.

15. *Parus griseiventris* (= *P. afer*): General in *Brachystegia* woodland on the west side, extending into south western Tanganyika, but unknown to the east of the Rift. Regarded

as a species distinct from *P. afer*, following Hall & Traylor (1959) and Irwin (1959).

16. *Parus leucomelas*: General in open country with scattered bushes on the west side, only extending around the north of Lake Nyasa to Njombe (Lynes, 1934).

17. *Nectarinia kilimensis*: Distribution as for the last species: mainly on the edges of evergreen forest, rarely below 4,500 feet.

18. *Antheptes anchietae*: On the west, extends south to Dedza, and Furancungu (Vincent, 1933). Inhabits mainly the margins of *Brachystegia* woodland. A monotypic species, ranging across from western Angola, and in Tanganyika only known from the extreme west (Moreau, 1947).

19. *Euplectes macrourus*: Extends south on the west to Dedza, in moist, spongy grasslands, only extending around the north end of Lake Nyasa to Njombe (Lynes, 1934).

Macronyx ameliae is not formally included above, since although it is unknown east of the Rift, and does occur to the west in the Ncheu, Dedza and Lilongwe Districts, its occurrence is patchy. At the north end of Lake Nyasa it occurs at the mouth of the Songwe River, and Alexander (1899) records it from Chicowa, in the Zambesi Valley west of Tete.

(2) *Occurring only on the eastern side (all forest species)*

1. *Buccanodon leucotis*: From Mlanje and Cholo to Zomba; also at Malawi. Range as a whole from Natal to Kenya.

2. *Apalis melanocephala*: In scattered localities throughout the eastern side, from Chiperoni and Mlanje to Songea, with a general range from Beira and eastern Southern Rhodesia through eastern Tanganyika to Kenya.

3. *Apalis chariessa*: From Cholo and Mlanje to Chikala, and at Chiperoni. Otherwise only known from the Uluguru Mts., Tanganyika and the Tana River in Kenya.

4. *Oriolus chlorocephalus*: From Cholo to Chikala, also at Chiperoni, and in scattered localities in eastern Tanganyika.

Coracina caesia is not formally included above, because although it is known from evergreen forest at Cholo, Chiradzulu, and Chiperoni, it also occurs west of the Shire River at Malawi (Long, 1959) and again at the extreme north end of Lake Nyasa (Bangs & Love-ridge, 1933). *Alethe choloensis* is another species difficult of formal inclusion. It is endemic to evergreen forests east of the Rift, in Nyasaland from Cholo and Mlanje to Mangoche, and as far east in Portuguese territory as Namuli. The genus is unrepresented in forests west of the Rift except by *A. fulleborni*, but ranging south only to about 11°.

B. SPECIES-PAIRS SEPARATED BY THE RIFT, OR SPECIES SHOWING SUBSPECIFIC DIFFERENCES ON THE TWO SIDES

1. *Tauraco persa*: This species, inhabiting mainly evergreen forest, is represented on the west by *T. p. schalowi*, on the east by *T. p. livingstonii*, though the latter extends around the north end of Lake Nyasa, the two forms occupying adjacent ground in the neighbourhood of the Songwe River. The Rift itself is practically entirely occupied by *T. porphyreolophus*, also found in plateau country to the west in the Mzimba and Karonga Districts, though the two species are almost entirely mutually exclusive. The foregoing is derived largely from Moreau (1958).

2. *Buccanodon whytii*: *B. w. sowerbyi* occurs in *Brachystegia* woodland west of the Rift from Dedza to the Mzimba District, being probably replaced in the Karonga District by *B. w. stresemanni*. On the east it is replaced by *B. w. whytii*, ranging north to Mangoche, and easily distinguished by the pattern of the crown and forehead. A form of evidently very similar head-pattern, *B. w. euroum*, occurs in the Songea District, also to the east of the Rift (Clancey, 1956).

3. *Pogoniulus (Viridibucco) leucomystax/simplex*: These two closely related monotypic

species are almost entirely separated by the Rift. Both are largely confined to evergreen forest. On the west, *P. leucomystax* is found from about 15° S., usually above 5,000 feet, and ranges north through Tanganyika, though absent from the extreme east, to central Kenya. On the east of the Rift it is only known from Njombe (Lynes, 1934). *P. simplex* occurs in Nyasaland on the east at Mangoche and Namizimu and sparsely within the Rift, to the east of the Shire River, near Fort Johnston in thickets. It is known from Sul do Save (Pinto, 1960), and in eastern Tanganyika and coastal Kenya.

4. *Phyllastrephus flavostriatus*: An evergreen forest species represented east of the Rift in southern Nyasaland and neighbouring Portuguese territory, and at Malawi, by *P. f. vincenti*, while on the west *P. f. alfredi* occurs as far south as Nchisi.

5. *Batis molitor soror*: According to Irwin (in ms. for *Ostrich*), *B. molitor* is the species to the west of the Rift, *B. soror* to the east. One or the other is widespread within the Rift, but their exact distribution requires further investigation. *B. soror* occurs at Mbamba Bay; *B. molitor* at Chinteché, and at Malawi and in surrounding lowlands only *B. molitor* occurs. Both occur in any type of open woodland.

6. *Bessonornis anomala*: This species is unaccountably absent from various localities where there is suitable habitat (evergreen forest) on the two sides of the Rift, but may perhaps be fairly included. On the east, *B. a. anomala* occurs at Mlanje, and at Chiperoni, while *B. a. grotei* occurs at Songea, and apparently intergrades around the north end of Lake Nyasa with *B. a. macleodii*, extending south on the west to the Vipya Plateau. See Moreau (1950).

7. *Apalis thoracica*: The striking feature of this case is that, associated with evergreen forest at Zomba and Mlanje, on the east of the Rift, there occurs the very richly coloured *A. t. flavigularis*, while on the west side, separated by only some fifty miles at the nearest point, there occurs the very distinct *A. t. whitei*. This case is all the more remarkable because White (1960c) regards *A. t. whitei* as a synonym of *A. t. arnoldi*, of eastern Southern Rhodesia, these two being much more widely separated from each other (by the Zambezi Valley) than is *A. t. whitei* from *A. t. flavigularis*. Further north on the west side of the Rift, on the Vipya and Nyika plateaux, there occurs *A. t. youngi*. Another anomaly may here be mentioned, in that to the west of the Luangwa Rift, in the Mpika and Serenje Districts, there occurs a population also identified by White (1960c) as *A. t. arnoldi*. Also, on the north-east side of the Rift, in the Songea District, there is a population assigned by Mackworth-Praed & Grant (1955) to *A. t. whitei*! Incidentally these authors, no doubt on account of the marked difference in intensity of pigment, place *A. t. flavigularis* in a different species from the other forms mentioned above.

8. *Camaroptera stierlingi*: According to Irwin (1960), *C. s. stierlingi* is the form to the east of the Rift, and also occurs at Malawi, while on the west it is replaced by *C. s. irwini*. The species does occur very sparingly within the Rift. Investigation is needed as to the subspecific status of such populations.

9. *Cisticola aberrans*: Following White (1960b), *C. emini* is conspecific with *C. aberrans*. *C. a. nyika* occurs throughout Nyasaland west of the Rift, usually among rocks in *Brachystegia* woodland. It is also found at Piri-longwe. East of the Rift it is replaced by *C. a. lurio*.

10. *Lanius collaris*: A case requiring further investigation and collecting, Benson (1953) gives *L. c. humeralis* for the whole of Nyasaland. But Benson & White (1957) give *L. c. capelli* for throughout Northern Rhodesia, and this may be the subspecies in Nyasaland west of the Rift, with *L. c. humeralis* confined to the east. The species occurs uncommonly as low as 1,500 feet in the Rift itself, and the subspecific status of such populations also requires investigation.

11. *Malaconotus (Chlorophoneus) olivaceus*: *M. o. makawa* inhabits evergreen forest to the west of the Rift, on the Kirk Range north to Chongoni. To the east, it is replaced by *M. o. bertrandi* at Mlanje, Zomba and Malosa.

12. *Malaconotus (Chlorophoneus) nigrifrons*: *M. n. sandgroundi* occurs in evergreen forest east of the Rift from Cholo and Mlanje to Mangoche. The species is absent west of the Rift south of the Nyika Plateau, where the subspecies is attributed by Rand (in Mayr & Greenway, 1960) to *M. n. nigrifrons*, ranging north to Kenya and around the north end of Lake Nyasa to Songea (Moreau & Southern, 1958).

13. *Anthreptes longuemarei*: *A. l. angolensis* occurs throughout west of the Rift, mainly in *Brachystegia* woodland, only extending to Lake Nyasa at Kota-kota and Karonga. East of the Rift, and at Piri-longwe, it is replaced by *A. l. nyassae*.

THE ALBERTINE RIFT

The Albertine Rift is formed by the lake chain from Lake Albert to the south end of Lake Tanganyika. Both sides of Lake Albert consist of a forest and savanna mosaic with the Lendu Plateau on the west side rising to summits over 7,000 feet. Between Lakes Albert and Edward the massif of Ruwenzori forms a high ridge on the east of the Rift, and the eastern side of the Rift forms an escarpment from east of Lake Albert to the highlands of Ruanda and Urundi. On the west from north-west of Lake Edward to the ridges west of Lake Kivu and north-west of Lake Tanganyika the edge of the Rift is more elevated rising to 10,000 feet. The southern end of this western ridge (Itombwe) with Mt. Mohi over 10,000 feet is followed by a depression formed by the Kilombwe River. South of this a further massif (Kabobo) rises to a little over 8,000 feet, and this is followed by the valley of the Lukuga River which runs into Lake Tanganyika at Albertville. Further south again is the plateau of Marungu, rising to about 6,000 feet.

South of the Urundi Highlands there are few high points on the east of Lake Tanganyika. The most important of these is the Kungwe Mahare mountains almost opposite Albertville and separated from the Urundi Highlands by the Malagarasi Valley. Further south and opposite the Marungu Highlands, there are the Ufipa Highlands on the east of the lake.

In considering the significance of the Albertine Rift discussion will be confined to passerine birds and mainly to those found in forest, montane, or lowland.

The Rift where it forms the boundary between the Congo and Uganda evidently forms no barrier for the passage of a great many forest birds which extend east in varying degrees into Uganda and western Kenya. There are however a number of cases of lowland forest birds which do not extend east of the Rift, and therefore are either unknown from Uganda or only recorded there from Bwamba on the west of Ruwenzori.

Examples are *Smithornis sharpei*, *Baeopogon clamans*, *Criniger barbatus*, *C. ndussumensis*, *Thescelocichla leucopleura*, *Chlorocichla simplex*, *Phyllastrephus icterinus*, *P. lorenzi*, *Nicator vireo*, *Turdus oberlaenderi*, *T. crossleyi* (if treated as specifically distinct from *gurneyi*), *Muscicapa olivascens*, *M. epulata*, *Pedilorkynchus tessmanni*, *Diaphorophya tonsa*, *Psaldiprocne nitens*, *Malaconotus cruentus*, *Dryoscopus sabinii*, *Nectarinia batesi*, *N. minulla*, *Ploceus albinucha*, *P. aureonucha*, *P. preussi*, *P. dorsomaculatus*, *Malimbus coronatus*, *M. nitens*, *M. erythrogaster*, *M. flavipes*, *Parmoptila woodhousei*, *Spermophaga poliopteryx*, *Nigrita luteifrons*, *N. bicolor*.

In the case of the lowland forest species which do cross the Rift, however, there is practically no subspecific difference between populations of west Uganda and the west side of the Rift, a conspicuous exception being however *Anthreptes collaris*. The Rift in this area at its northern end thus presents an anomalous picture. On the one hand it has evidently proved no obstacle to the numerous lowland birds, the Uganda populations not even being sufficiently isolated to have developed subspecific variations. On the other hand about 32 lowland forest passerines have failed to cross the Rift.

Turning to montane forest species, the only montane areas on the north-east rim of the Rift in the north are provided by Ruwenzori and Kigezi. Ruwenzori is slightly anomalous, since although strictly part of the eastern side of the Rift, the Rift bifurcates slightly to its

south to take in Lake George. Unknown from the mountain forests east of the Rift in this area are *Pseudocalymptomena graueri*, *Lioptilus rufocinctus*, *Graueria vittata*, *Hemitesia neumanni*, *Cossypha roberti*, *Malaenornis ardesiaca*, *Muscicapa lendu*, *Prionops alberti*, *Nectarinia rockefelleri*. Some of these however do occur east of the Rift further south in the Rugege forest area of Ruanda, and may perhaps be found eventually in Kigezi.

Ruwenzori itself is the focus of a small amount of rather slight subspecific differentiation in its montane birds, having peculiar forms of *Phylloscopus umbrovirens*, *Nectarinia alinae*, *N. regia* and *N. afra*. The amount of subspecific variation due to any isolation of Ruwenzori is thus less than the peculiarities of absent species occurring in the adjacent Rift Valley mountains west and south.

West of the Rift in this area the main peculiarity is furnished by the isolated position of the Lendu plateau west of Lake Albert. Some montane species occurring in the main chain further south are absent there (e.g. *Graueria*, *Cossypha roberti*, *C. bocagei*, *Alethe archeri*, *Lioptilus rufocinctus*, *Parus fasciiventer* etc). One or two subspecies (e.g. *Muscicapa l. lendu*, *Sylvietta leucophrys chapini*, *Dioptrornis chocolatina demicincta*) are peculiar to the Lendu plateau. Since it occupies an isolated position at the northern extremity of the western wall of the Rift, and apparently the forest has been extensively destroyed on the Lendu plateau, it is not surprising that it should have a somewhat impoverished montane fauna, although it is perhaps poorer than might have been suspected from its position.

Further south from west of Lake Edward to Itombwe the forest fauna of the western side of the Albertine Rift exists in its most developed form. A considerable number of the species of this fauna have been able to cross the gap caused by the Kilombwe river, and reappear on Mt. Kabobo in identical or distinguishable forms. Absent south of the Kilombwe however are *Pseudocalymptomena graueri*, *Coracina graueri*, *Graueria vittata*, *Sheppardia aequatorialis*, *Cossypha roberti*, *Malaenornis ardesiaca*, *Malaconotus multicolor*, *Malaconotus lagdeni*, *Poeyoptera stuhlmanni*, *Cinnyricinclus sharpii*, *Nectarinia purpureiventris*, *Ploceus insignis* and *Linurgus olivaceus*. Some other absent species are attributable to the fact that Kabobo is not high enough for them. A standard comparative list of montane species, mainly forest, is difficult to draw up since opinions will differ as to the inclusion of certain species. The list which we have used contains 64 passerine species associated with the main area of the western chain on the Congo side of the Rift. About two thirds of these occur also on both Ruwenzori and on Mt. Kabobo, so that the gap south of Itombwe is faunistically as important as the Rift west of Ruwenzori in terms of being a species barrier. If subspecific variation is also taken into account this is greater on Kabobo than on Ruwenzori, so that the Kilombwe valley appears to be a greater isolating factor than the Rift west of Ruwenzori.

The Lendu plateau is decidedly poorer than either Kabobo or Ruwenzori, apparently only possessing about half of the 64 species.

Three montane areas remain for comment. Of these Kungwe Mahare is the most important as it might be regarded as an outlier of the main Rift chain ridges on the south, mid way down Lake Tanganyika. However its montane fauna, although interesting, is very deficient in species as compared with the main western chain. Out of the standard list of 64 species, only 16 are known to occur on Kungwe. Kungwe is isolated by Lake Tanganyika from Mt. Kabobo, and judging by the great absence of species of Mt. Kabobo, the lake forms a major barrier. However the gap between the Urundi highlands and Kungwe is evidently equally a barrier. Ufipa and the Marungu highlands are even poorer. On Marungu the presence of *Apalis pulchra*, *A. binotata*, and *Nectarinia afra*—all found in the western Rift chain, but not on Ufipa—suggests that Marungu may have derived a very scanty part of its fauna from the Rift chain. Ufipa has no elements to suggest any close connection with the Rift chain, and has a fauna more closely related to other East African mountains.

The overall conclusion is that the Albertine Rift like any other ecological gap presents a barrier to the dispersal of species but its significance is less than might be supposed. The faunas of Kabobo and the Rendu plateau, though separated from the main western montane chain by less striking physical features than the Albertine Rift, show similar deficiencies in their fauna as compared with the main chain. Kungwe with the double barriers of an unsuitable land gap to the north and a water gap to the west has few of the possibly expected species, whilst the southern massifs of Marungu and Ufipa, although part of the Rift valley system are evidently too isolated to belong faunally to the montane fauna of the main chain.

In considering the poor faunas, relatively speaking, of Kungwe, Marungu and Ufipa, a further factor should be taken into account in addition to the physical isolating factors. All three have much smaller areas of forest to provide niches for species than the areas further north. In this respect they are analogous to small islands as distinguished from larger islands in insular faunas, and their reduced size must in itself be a limiting factor. Secondly they lack the altitude of the main more northern areas, another limiting factor; this however is less serious, in all probability, than size and isolation, since Kabobo is no higher but has an incomparably richer fauna.

The foregoing account of the Albertine Rift is derived largely from Chapin (1932: 54); Moreau (1943), for Kungwe and Ufipa; and Prigogine (1960), for Kabobo.

THE KENYA RIFT VALLEY

The profile of west and central Kenya may be described as follows: (i) the eastern shore of Lake Victoria and the country north of it, which includes some forest areas; (ii) the high ridge of the Mau escarpment and Mt. Elgon, forming the west rim of the Rift valley; (iii) the trough of the Rift, much drier than the foregoing; (iv) the central highlands of Kenya east of the Rift. These form the east rim of the Rift. The two rims of the Rift contain considerable montane forest.

For birds extending east from Uganda where except on the Uganda rim of the Albertine Rift, forest is lowland, there are thus two obstacles. The first of altitude provided by the Mau escarpment, and the second of aridity provided by the Rift in Kenya. That one or other of these factors is an obstacle is clear, since many species found in Uganda extend east no further than west Kenya. There are however a few anomalous cases such as *Mala-cocincla rufipennis* and *Neocossyphus rufus*, which occur both in lowland East Africa and in Uganda or West Kenya, and have evidently crossed both the montane highlands and the Rift Valley.

Unlike the Albertine Rift, the Kenya Rift is not only an obstacle to the passage of certain species, but also an isolating factor which has resulted in subspeciation of a number of species which occur on either side of it. About twenty such instances occur among passerine birds, of which the following may be cited as examples.

Species	Western Form	Eastern Form
<i>Mirafrax rufocinnamomea</i>	<i>kavirondensis</i>	<i>torrida</i>
<i>Phyllastrephus fischeri</i>	<i>cabanisi</i>	<i>placidus</i>
<i>Alethe poliocephala</i>	<i>carruthersi</i>	<i>akeleyae</i>
<i>Turdus piaggiae</i>	<i>piaggiae</i>	<i>kilimensis</i>
<i>Eremomela scotops</i>	<i>citriniceps</i>	<i>kikuyensis</i>
<i>Laniarius ferrugineus</i>	<i>major</i>	<i>ambiguus</i>
<i>Zosterops senegalensis</i>	<i>jacksoni</i>	<i>kikuyuensis</i>
<i>Nectarinia olivacea</i>	<i>vincenti</i>	<i>neglecta</i>
<i>Ploceus ocularis</i>	<i>crocatus</i>	<i>suahelicus</i>
<i>Serinus burtoni</i>	<i>gurneti</i>	<i>albifrons</i>

The genus *Platysteira* presents an interesting example of two species forming a super-species in which not the Rift, but apparently competition provides the isolating factor, since *P. peltata* occurs on both sides of the Rift, but only in the escarpment in the west, being replaced at lower levels by *cyanea*. *Turdus piaggiae* and *gurneyi*, a closely related species-pair are somewhat analogous, since *gurneyi* does not cross to the west of the Rift in Kenya, whilst *piaggiae* does cross to the east as far as the central highlands of Kenya.

Considering how pronounced a physical feature the Kenya Rift valley is, its effect in permitting subspeciation between populations of the same species on either side of it are not very striking, although its effect as a total barrier to species dispersal is obvious. However we have seen that the Albertine Rift, a less extreme barrier has an equally marked effect. In addition any obstacle to continuous distribution is likely to affect species dispersal, as shown by the isolation of such localities as the Lendu plateau and Mt. Kabobo in relation to the main chain of the western rim of the Albertine Rift. This would suggest that Rift valleys are merely one of the various ways in which populations may be isolated by the existence of an unsuitable environment between them. The Kenya Rift, because it presents such an obvious barrier, might be expected to have had a more pronounced effect than in fact seems to be the case, since equally marked effects can be associated with less spectacular barriers. Overall then, the significance of an apparent barrier depends less on the extreme nature of the contrasting environment than on the ability or inability to cross it. Thus *Laniarius* forms and *Phyllastrephus* forms cited above do in fact intergrade, showing that gene flow is not completely prevented by the existence of the Rift. The water barrier of Lake Tanganyika seems to be a more effective barrier to movement between Kabobo and Kungwe than the unfavourable land barrier of the Kenya Rift.

The foregoing account of the Kenya Rift is derived largely from Jackson & Sclater (1938).

GENERAL DISCUSSION AND CONCLUSIONS

Apart from the isolating factors which, as mentioned in the introduction, affect distribution of species and give rise to discontinuous populations as a result of rift and river valley conditions, the following points merit mention:—

(1) Considering *Brachystegia* woodland, it is particularly noteworthy that out of the Luangwa list of 22 species largely confined to the west of that Rift, only two are associated with this habitat. It is relatively easy for them to extend further west, around the northern end. There are however a further 10 species largely confined to the west of the Nyasa Shire Rift (see list A (1) thereunder, Nos. 1, 6, 7, 8, 9, 11, 12, 13, 15, 18). By contrast, there is not a single *Brachystegia* species confined to the east of these two Rifts, if *Ploceus olivaceiceps* is excluded, probably ecologically analogous to *P. angloensis*. Possibly the main centre of evolution of such species has been west of the Luangwa Rift. All of those mentioned range to western Angola. It is also noteworthy that there are eleven species listed from north of the Zambezi but unknown in Southern Rhodesia (one of them occurs in the Sul do Save). By contrast, there is not a single one occurring in Southern Rhodesia which does not reappear north of the Zambezi. *Brachystegia* is unknown south of the Limpopo, with the result that the Zambezi list A (1) contains 15 species associated with this habitat. Subspeciation concerns nine *Brachystegia* woodland species (considering the Zambezi, Luangwa and Nyasa Shire lists as a whole).

(2) Turning to the other most important habitat (evergreen forest, including edges), only four species do not range north of the Limpopo. Of these, this only applies really strictly to *Cossypha dichroa*, the other three (*Mesopicos*, *Lioptilus* and *Scrinus scotops*) all being represented north of the Zambezi. On the other hand there are seven species not extending south of the highlands of eastern Southern Rhodesia, two of which (*Pogonochela swynnertonii* and *Prinia robertsi*) are endemics, and a third (*Apalis melanocephala chirindensis*) at least a well

marked endemic subspecies. The number of species confined to the north of the Zambezi is 15, and could be increased very considerably if species occurring in northern Nyasaland and the north of Northern Rhodesia (for which of course there is no evidence that the Zambezi Valley is acting as a barrier) were added. According to Moreau (1952: 594) only 16 out of the 116 African montane forest passerine species occur south of the Zambezi. By contrast to *Brachystegia* woodland, there are 10 species (including *Coracina caesia* and *Aethya* spp., not extending west of the Luangwa Rift or even the Nyasa Shire Rift (see the respective lists A (2)). Thus speciation in this eastern area may have been more active in the case of evergreen forest than *Brachystegia* species. Subspeciation is much more marked than in the case of *Brachystegia*, and concerns 20 species. There are however some curious anomalies in both ecological categories, as already mentioned. Thus one must postulate a recent connection (evergreen forest in a colder regime—presumably via the humid littoral of Portuguese East Africa) to explain the existence of identical populations of *Andropadus milanensis* in eastern Southern Rhodesia and north of the Zambezi at Mlanje, Chiperoni and Namuli (see Zambezi list B). Furthermore, at the end of the Zambezi list there is a long list of species in various ecological categories for which there is neither any present evidence of any gene flow nor of subspeciation. In this connection the reader is referred to Zeuner (1950, 1959), for a discussion of climatic oscillations.

(3) Attention should be drawn to the case of several species found south of the Limpopo and absent from Southern Rhodesia, yet reappearing north of the Zambezi. It has already been suggested in the case of *Mesopicos griseocephalus* that this might be due to competition with *Campethera abingoni*. Again, in the case of *Anthus leucophrys*, *A. vaalensis* or *A. novae-seelandiae* might be the competitor, and in the case of *Cisticola textrix*, *C. aridula*, as already suggested by Benson and White (1961). *Serinus scotops*, apparently closely related to *S. citrinelloides*, presents a different problem, as there is no analogue in Southern Rhodesia. In the Zambezi list A (1), there are the cases of *Columba guinea* and *Eurocephalus anguimitens* unknown in Northern Rhodesia and Nyasaland, but reappearing in the Rukwa Valley. They both seem to have a preference for semi-arid country and the appropriate conditions for their occurrence apparently do not at present exist in this intervening area.

(4) Formally included in the Limpopo, Zambezi, Luangwa and Nyasa/Shire lists are only 20 non-passerine species compared to 127 passerines. The highest totals for the latter are Sylviidae (30) and Turidae (18). Even the Hirundinidae (four) are represented.

ACKNOWLEDGEMENTS

We are especially grateful to Mr. A. Angus, of the Agricultural Research Station, Mt. Makulu, Northern Rhodesia, and Mr. G. J. Snowball, of the Department of Geological Survey, Northern Rhodesia, for advice on ecological and geological matters, respectively.

REFERENCES

- ALEXANDER, B. 1899. An ornithological expedition to the Zambezi River. Part 1. *Ibis*, 41: 549–583.
 ANONYMOUS. 1960. Atlas de Moçambique. Lourenço Marques.
 BANGS, O. and LOVERIDGE, A. 1933. Report on the scientific results of an expedition to the south-western highlands of Tanganyika Territory. 3. Birds. *Bull. Mus. Comp. Zool. Harv.*, 75: 143–221.
 BENSON, C. W. 1950. A collection from Chiperoni Mountain, Portuguese East Africa. *Bull. Brit. Orn. Cl.*, 70: 51.
 BENSON, C. W. 1953. A check list of the birds of Nyasaland, Blantyre and Lusaka.
 BENSON, C. W. 1955a. New forms from Central Africa. *Bull. Brit. Orn. Cl.*, 75: 101–109.
 BENSON, C. W. 1955b. A note on *Pirenestes Swainson*, and description of a new species. *Bull. Brit. Orn. Cl.*, 75: 109–110.
 BENSON, C. W. 1958. Some additions and corrections to a Check List of the birds of Northern Rhodesia. *Occ. Papers Nat. Mus. S. Rhod.*, 22B: 190–197.

THE SIGNIFICANCE OF VALLEYS AS AVIAN ZOOGEOGRAPHICAL BARRIERS

- BENSON, C. W. 1959. Some additions and corrections to a *Check List of the birds of Northern Rhodesia* No. 2. *Occ. Papers Nat. Mus. S. Rhod.*, 23B: 257-285.
- BENSON, C. W. 1960a. Recent records from north-western Northern Rhodesia. *Bull. Brit. Orn. Cl.*, 80: 106-112, 114-119.
- BENSON, C. W. 1960b. Some additions and corrections to a *Check List of the birds of Northern Rhodesia*. No. 3. *Occ. Papers Nat. Mus. S. Rhod.*, 24B: 343-350.
- BENSON, C. W., BOULTON, R. and IRWIN, M. P. STUART. 1961. Some records from the Mpika and Serenje Districts, Northern Rhodesia. *Bull. Brit. Orn. Cl.*, 81: 3-5.
- BENSON, C. W., IRWIN, M. P. STUART and WHITE, C. M. N. 1959. Some aspects of speciation in the birds of Rhodesia and Nyasaland. *Proc. First Pan-Afr. Orn. Congr.*: 397-414.
- BENSON, C. W. and WHITE, C. M. N. 1957. Check list of the birds of Northern Rhodesia Lusaka.
- BENSON, C. W. and WHITE, C. M. N. 1961. Discontinuous distributions (Aves). *Proc. Fed. Sci. Congr.*, in press.
- BRELSFORD, W. V., Ed., 1960. Handbook to the Federation of Rhodesia and Nyasaland. Salisbury.
- CHAPIN, J. P. 1932-54. The birds of the Belgian Congo. *Bull. Amer. Mus. Nat. Hist.*, 65, 75, 75A, 75B.
- CLANCEY, P. A. 1956. Miscellaneous taxonomic notes on African birds. *Durban Novit.*, 4 (15): 245-256.
- CLANCEY, P. A. 1960. Fourth report of the S.A.O.S. List Committee. *Ostrich*, 31: 64-77.
- DUKEY, F. 1931. Physical map of Nyasaland. Zomba.
- FLINT, R. F. 1959. Pleistocene climates in eastern and southern Africa. *Bull. Geol. Soc. Amer.*, 70: 343-374.
- HALL, B. P. 1956. Notes on a small collection of birds from Panda Matenga, N. E. Bechuanaland. *Ostrich*, 27: 96-109.
- HALL, B. P. 1960. The ecology and taxonomy of some Angola birds. *Bull. Brit. Mus. (Nat. Hist.)*, 6: 367-453.
- HALL, B. P. and TRAYLOR, M. A. 1959. The systematics of the African Grey Tits, *Parus afer* and *Parus griseiventris*. *Bull. Brit. Orn. Cl.*, 79: 42-46.
- HEINRICH, G. 1958. Zur verbreitung und lebensweise der vögel von Angola. *Journ. Ornith.*, 99: 121-141, 322-362, 399-421.
- IRWIN, M. P. STUART. 1956. Field notes on a collection from Mozambique. *Ostrich*, 27: 28-39.
- IRWIN, M. P. STUART. 1958. The relationships of the races of the Cape Bunting, *Fringillaria capensis* in the Rhodesias and Nyasaland. *Bull. Brit. Orn. Cl.*, 78: 69-71.
- IRWIN, M. P. STUART. 1959. The specific relationship of *Parus afer* and *Parus griseiventris*. *Bull. Brit. Orn. Cl.*, 79: 46-48.
- IRWIN, M. P. STUART. 1960. Relationships within the *Camaroptera fasciolata*-stierlingi- simplex complex of warblers. *Durban Mus. Novit.*, 6 (3): 47-60.
- JACKSON, F. J. and SCLATER, W. L. 1938. The birds of Kenya Colony and the Uganda Protectorate. London.
- KEAY, R. W. J. et al. 1959. Vegetation map of Africa. Oxford.
- KING, L. C. 1951. South African scenery. London.
- LAMM, D. W. 1953. Comments on certain records from northern Sul do Save, Mozambique. *Ostrich*, 24: 2-8.
- LONG, R. C. 1959. Recent interesting species in the Port Herald District, Nyasaland. *Ostrich*, 30: 136-137.
- LONG, R. C. 1960-61. The birds of the Port Herald District. *Ostrich*, 31: 85-104; 32: 23-35.
- LYNES, H. 1934. Contribution to the ornithology of southern Tanganyika Territory. *Journ. Ornith.*, 82, Sonderheft.
- MACDONALD, J. D. 1958. Note on *Cinnyris manoensis* Reichenow. *Bull. Brit. Orn. Cl.*, 78: 7-9.
- MACKWORTH-PRAED, C. W. and GRANT, C. H. B. 1955. Birds of eastern and north-eastern Africa. 2. London.
- MAYR, E. and GREENWAY, J. C., Ed. 1960. Check-List of the birds of the World. 9. Cambridge, Mass.
- MCCONNELL, R. B. 1951. Rift and shield structure in East Africa. *Internat. Geol. Congr. Rep't. 18th Sess.*, 14: 199-207.
- MCLACHLAN, G. R. and LIVERSIDGE, R. 1957. Roberts' birds of South Africa. Cape Town.
- MEISE, W. 1937. Zur vogelwelt des Matengo-Hochlandes nahe dem nördende des Njassasees. *Mit. Zool. Mus. Berlin*, 22: 86-160.
- MOREAU, R. E. 1943. A contribution to the ornithology of the east side of Lake Tanganyika. *Ibis*, 85: 377-412.
- MOREAU, R. E. 1947. A contribution to the faunistics of Tanganyika Territory. *Ibis*, 89: 216-231.
- MOREAU, R. E. 1950. A "stepped cline" in *Bessonomis*. *Ibis*, 92: 642-643.
- MOREAU, R. E. 1951. Geographical variation and plumage sequence in *Pogonocichla*. *Ibis*, 93: 383-401.
- MOREAU, R. E. 1952. Africa since the Mesozoic: with particular reference to certain biological problems. *Proc. Zool. Soc. Lond.*, 121: 869-913.
- MOREAU, R. E. 1958. Some aspects of the Musophagidae. *Ibis*, 100: 67-112, 238-270, 620.
- MOREAU, R. E. and SOUTHERN, H. N. 1958. Geographical variation and polymorphism in *Chlorophoneus* shrikes. *Proc. Zool. Soc. Lond.*, 130: 301-328.
- PEDRO, J. G. and BARBOSA, L. A. G. 1955. Esboço do reconhecimento ecológico-agrícola de Moçambique, 2 (5): 69-224.
- PINTO, A. A. DA ROSA. 1960. Some new records of birds for the Sul do Save region and Moçambique. *S. Afr. Journ. Sci.*, 56: 37-38.

- PINTO, A. A. DA ROSA and LAMM, D. W. 1953-56. Contribution to the study of the ornithology of Sul do Save (Mozambique). *Mem. Mus. Dr. Alr. Castro*, 2-4.
- PRIGOGINE, A. 1960. La faune ornithologique du massif du Mount Kabobo. *Ann. Mus. Roy. Congo Belge*, 85: 7-46.
- SASSI, M. and ZIMMER, F. 1941. Beiträge zur Kenntnis der vogelwelt des Songea Distriktes mit besonderer berücksichtigung des Matengo-Hochlandes. *Ann. Naturhist. Mus. Wien*, 51: 236-346.
- SCLATER, W. L. 1911. On the birds collected by Mr. Claude H. B. Grant at various localities in South Africa. Part 3. *Ibis*, 53: 695-741.
- SMITHERS, R. H. N., IRWIN, M. P. STUART and PATERSON, M. L. 1957. A check list of the birds of Southern Rhodesia. Cambridge, England.
- SMITHERS, R. H. N., IRWIN, M. P. STUART and PATERSON, M. L. 1959. Additions and corrections to A Check List of the birds of Southern Rhodesia. *Occ. Papers Nat. Mus. S. Rhod.*, 23B: 232-256.
- TRAPNELL, C. G. 1953. The soils, vegetation and agriculture of north-eastern Rhodesia. Lusaka.
- TRAPNELL, C. G. and CLOTHIER, J. N. 1957. The soils, vegetation and agricultural systems of north-western Rhodesia. Lusaka.
- TRAPNELL, C. G., MARTIN, J. D. and ALLAN, W. 1948. Vegetation-soil map of Northern Rhodesia. Lusaka.
- TRAYLOR, M. A. 1960. Notes on the birds of Angola, non-passeres. *Mus. Dundo. Subsid. estud. biol. Lunda*: 131-186.
- VAN DER MERWE, N. J. and PIENAAR, D. 1959. A preliminary list of the birds of The Percy Fyfe Nature Reserve. *Ostrich*, 30: 130-133.
- VERHEYEN, R. 1953. Exploration du Parc National de l'Upemba. Fasc. 19. Brussels.
- VESLY-FITZGERALD, L. D. E. F. and BEESLEY, J. S. S. 1960. An annotated list of the birds of the Rukwa Valley, S. W. Tanganyika. *Tang. Notes and Records*, 54: 91-110.
- VINCENT, J. 1933-36. The birds of northern Portuguese East Africa. *Ibis*, 75-78.
- VINCENT, J. 1952. A Check List of the birds of South Africa. Cape Town.
- WHITE, C. M. N. 1957. Taxonomic notes on Northern Rhodesia birds. *Bull. Brit. Orn. Cl.*, 77: 34-36.
- WHITE, C. M. N. 1960a. On *Cisticola chiniana procera* Peters. *Bull. Brit. Orn. Cl.*, 80: 88-89.
- WHITE, C. M. N. 1960b. Notes on some savanna species of the genus *Cisticola*. *Bull. Brit. Orn. Cl.*, 80: 128-130.
- WHITE, C. M. N. 1960c. Further notes on African warblers. *Bull. Brit. Orn. Cl.*, 80: 147-152.
- WHITE, C. M. N. 1960d. A check list of the Ethiopian muscipidae (Sylviinae). *Occ. Papers Nat. Mus. S. Rhod.*, 3 (24B): 399-430.
- WHITE, C. M. N. 1961. The African rough-winged swallows. *Bull. Brit. Orn. Cl.*, 81: 29-33.
- WINTERBOTTOM, J. M. 1959a. Some zoo-geographical remarks on the South African avifauna. *Proc. First Pan-Afr. Orn. Congr.*: 40-46.
- WINTERBOTTOM, J. M. 1959b. Review of the races of the Cape Wagtail, *Motacilla capensis* L. *Bull. Brit. Orn. Cl.*, 79: 96-98.
- ZEUNER, F. W. 1950. Dating the Past. 2nd edition. London.
- ZEUNER, F. W. 1959. The Pleistocene Period. London.

DISCUSSION

- Mr. Liversidge*: Chapin suggests that the savannah fauna is derived from a forest fauna, and I have been struck by the absence of endemic species in the arid regions of South West Africa.
- Mr. Stuart Irwin*: I do not believe that the forests of Africa were very much greater in the past than they are today, and think that much was always covered by savannah.
- Dr. Stuckenberg*: There is evidence of a considerable increase in the Congo forests in the past 12000 years and parts are believed to be of very recent origin.
- Dr. Winterbottom*: While I would not dispute that *Brachystegia* has many forms peculiar to it, I think the authors tend to overemphasize this and so obscure the fact that it also has many species in common with other types of woodland, some of these extending well down into the Transvaal.
- Mr. Stuart Irwin*: I agree that there are many species which one cannot use in trying to determine the past significance of physical barriers.
- Dr. Winterbottom*: If there are so many species which cannot be used, it seems doubtful whether the distinction is real or important.

THE SIGNIFICANCE OF VALLEYS AS AVIAN ZOOGEOGRAPHICAL BARRIERS

Prof. Ewer: There is again confusion between the "lumpers" and the "splitters". Irwin has shown how a study of species which respect barriers can reveal something of the history of the fauna; but wide-ranging species do not show anything comprehensible.

Mr. Attwell: Is there any case of a river acting as a barrier to avian dispersal in the areas considered?

Mr. Stuart Irwin: While no positive instance is known, *Francolinus hildebrandti* occurs on the north side of the Zambezi and *F. natalensis* on the south side at Tambara. It has been suggested that the birds are conspecific and the river may be a barrier between the two forms which are probably very sedentary. In the Balovale district the two sides of the Zambezi show marked contrasts in avifauna which must, however, be attributed to equally marked differences in the environment, as *Brachystegia* woodland predominates in the east and open plains in the west. Lake Mwera-Wa-Ntipa may also act as a barrier in certain respects, probably through lack of the correct ecological conditions for certain forms.

Prof. van Zinderen Bakker: In considering this problem, one must remember that conditions were generally hotter and more arid during the Tertiary. Botanically, the Moçambique plain does not conform well to the pattern of *Brachystegia* woodland elsewhere.

Mr. Stuart Irwin: The same applies to the avifauna, and temperature appears to be a limiting factor, since the highland forms do not generally come down into the *Brachystegia* woodlands of the plain.